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BULLETIN OF THE TORREY BOTANICAL CLUB
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DISTRIBUTION AND NATURE OF POLYPLOIDY IN FESTUCA ELATIOR L.[1]

W. M. MYERS AND HELEN D. HILL[2]

In the past the plant breeder has dealt in most cases with species all or nearly all plants of which had a constant chromosome number. Rare deviations which occurred were hypo- or hyperploids or polyploids that arose in experimental material. In many species of the plant kingdom, however, races with different chromosome numbers have been reported as occurring naturally. The phenomenon of intraspecific chromosome races was considered in detail by Müntzing (1936) who concluded that more than 100 cases were known in the Angiosperms.

In a recent survey of the literature of *Gramineae*, Myers (in press) found 99 grass species in which two or more intraspecific chromosome races had been reported. This number does not include several species, such as *Poa pratensis*, in which apomixis occurs and results in perpetuation of aneuploid chromosome numbers nor species in which the variability may be conditioned by the high degree of polyploidy, as in *Alopecurus alpinus* and *A. antarcticus*. Among the species with intraspecific chromosome races are some of the most important forage grasses including *Phleum pratense*, *Bromus inermis*, *B. marginatus* (*B. carinatus*), *Festuca elatior*, *Agropyron cristatum*, *A. smithii*, *Phalaris arundinacea*, *Andropogon furcatus*, and others. An extreme case of intraspecific polyploidy has been reported in *Panicum virgatum* by Nielsen (1944) who found 2n numbers of 18, 36, 54, 72, 90, and 108 chromosomes (2x, 4x, 6x, 8x, 10x, and 12x). Among 17 collections from an area of not more than 10 acres near Chippewa Falls, Wisconsin, 2x, 4x, 6x, 8x, and 10x forms were found.

Intraspecific polyploidy is of frequent occurrence in the genus *Festuca*, the condition having been found in six species and particularly in *F. elatior*, *F. rubra*, and *F. ovina*. In *F. elatior*, the diploid chromosome number of 14 was reported for European material by Kattermann (1930), Litardière (1923), and Stolze (1925), and for North American collections by Church (1936) and Nielsen and Humphrey (1937). Somatic numbers of 14 and 42 were reported by Nakajima (1930, 1931) and Evans (1926). The most detailed investigations of chromosome number in *F. elatior* were those of

[1] Contribution No. 81 of the U. S. Regional Pasture Research Laboratory, Division of Forage Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, U. S. Dept. of Agriculture, State College, Pa., in cooperation with the northeastern states.

[2] Geneticist and Scientific Aid, respectively.

Levitskii and Kuzmina (1927) and Stählin (1929). Their results are summarized in table 1.

TABLE 1. *Chromosome numbers in Festuca elatior according to Levitskii and Kuzmina (L&K) and Stählin (S).*

Subspecies and Variety	2n Chromosome Number	Authority
Subspecies *pratensis*		
var. *genuina* Hack. (var. *eu-pratensis* St.Y.)	14	L&K, S.
var. *apennina* Hack.	42	S.
Subspecies *arundinacea* Hack.		
var. *genuina* Hack. (var. *eu-arundinacea* St.Y.)	42	L&K, S.
var. *Fenas* Hack. (*glaucescens* Boiss.) subvar. *corsica* Hack.	42	L&K.
var. *Uechtritziana* (Wiesbaur) Hack.	14, 28	S.
var. *Letourneuxiana* St.Y. subvar. *Pitardii*	70	L&K.
var. *Cirtensis* St.Y.	70	L&K.

According to Levitskii and Kuzmina (1927) these cytologically different races are frequently difficult to distinguish morphologically and can be separated accurately only by determination of the chromosome numbers. In North America, Hitchcock (1935) recognized two forms, *Festuca elatior* L., meadow fescue, and *F. elatior* var. *arundinacea* (Schreb.) Wimm., tall fescue. These two forms are considered by agronomists to be adapted to somewhat different conditions, tall fescue, although tolerant of moist conditions, being more drouth resistant and better adapted to infertile soils than meadow fescue. When grown under comparable conditions in field plots, as spaced plants in the breeding nursery, or in greenhouse pots, the tall fescue plants are in general rather readily distinguishable from meadow fescue by their greater height, more robust appearance, and the greater size of vegetative and flower parts. Furthermore, it has been found (Kreitlow & Myers, in press) that meadow fescue plants are predominantly susceptible and tall fescue plants predominantly immune or resistant to crown rust, *Puccinia coronata*. Because of the importance of a knowledge of chromosome numbers and interrelationship of plants to be used in a breeding program, a cytological study of material collected from natural habitats and of existing strains of tall and meadow fescue was conducted.

COLLECTIONS FROM NATIVE STANDS

Festuca elatior is a native of Eurasia introduced into North America, and is now widely distributed in much of the northeastern region, occurring particularly in moist locations along roadsides, in lowland pastures, and occasionally in higher and somewhat drier locations. During the summer of 1941, individual panicles were collected from 24 locations in Centre County, Pennsylvania, and the chromosome number was determined of one plant

obtained from seed from each panicle. The chromosome numbers were determined from root-tips prepared for study by the methods described by Hill and Myers (1945).

Fourteen collections (a total of 166 single panicles) were obtained from the Spring Creek drainage area in the vicinity of State College. Nine of these collections (94 panicles) were from roadsides and permanent pastures adjacent to and subject to overflow from the creek during floods. All plants examined were diploid, 2n = 14, and, when grown in the nursery, were classified as meadow fescue types. Five collections (72 panicles) were from dry hillside locations. In general, the distribution of fescue plants was continuous, the stand becoming thinner with increased distances from Spring Creek. In four of these collections, all of the plants examined were diploid, 2n = 14, and meadow fescue type. One collection of 20 panicles was made in an area separated from the population of fescue adjacent to Spring Creek by a road and farmstead.[3] All of the plants examined from seed obtained from these panicles were hexaploid, 2n = 42, and in general could be classified in the breeding nursery as tall fescue types. Some plants, however, were not distinctly different in size and robustness from meadow fescue.

Four collections, two (19 panicles) from high ground and two (21 panicles) from low wet locations in the area east and north of Centre Hall, Pennsylvania, produced only diploid, 2n = 14, plants of meadow fescue type. Similarly a collection (12 panicles) near Potters Mills, Pennsylvania, and one (15 panicles) near Boalsburg, Pennsylvania, both from low areas, were diploid, as also were two collections (23 panicles) from high, dry locations and one (14 panicles) from a bottomland pasture near Stormstown, Pennsylvania. A single plant found in a clearing on the summit of Tussey Mountain above Pine Grove Mills, Pennsylvania, was hexaploid.

It is apparent from these results that both diploid and hexaploid types of *Festuca elatior* occur in natural stands in central Pennsylvania, the diploid, however, being considerably more common. Only fragmentary information is available regarding the distribution of these forms elsewhere in this country. Church (1936) and Nielsen and Humphrey (1937) reported only diploids in their studies. In the course of the present investigations, three collections of panicles from near Orono, Maine, were received from Doctor F. H. Steinmetz, and all plants examined from the seed were diploid. A fourth collection, obtained two years later by Doctor Steinmetz from one of the same meadows, proved to be uniformily hexaploid.

CHROMOSOME NUMBERS OF VARIETIES

Twenty plants were established from each of seven varieties of *Festuca elatior* included in the Uniform Grass Nurseries and the chromosome num-

[3] The authors are indebted to Professor J. K. Thornton, Department of Agronomy, The Pennsylvania State College, for this collection which was made on his farm.

bers were determined from root tip preparations.[4] In the following four varieties, classified as meadow fescue types, all plants were diploid:

1. English grazing strain, S–53, from the Welsh plant Breeding Station, seed increased at the Soil Conservation Service Nursery, Big Flats, New York.
2. Svalöf Early Meadow Fescue, seed increased at the Massachusetts Agricultural Experiment Station.
3. Otofte, seed increased at the Massachusetts Agricultural Experiment Station.
4. Minnesota No. 1449, selection from northern grown commercial seed.

In the following three varieties, classified as tall fescue types, all plants were hexaploid:

1. No. 2659 from Soil Conservation Service Nursery, Ithaca, New York, the seed originally obtained from England.
2. Alta fescue, F. C. 29,366, developed at the Oregon Agricultural Experiment Station.
3. Kentucky No. K–31, developed at Kentucky Experiment Station.

MEIOSIS IN DIPLOID AND HEXAPLOID TYPES

Meiotic behavior was studied in the microsporocytes of three diploid and six hexaploid plants. The material for study was collected from plants grown in greenhouse pots and was fixed in acetic alcohol. All data were collected and photomicrographs made from fresh aceto-carmine smear slides.

The diploid plants were generally regular in meiosis (table 2). Seven bivalents were found in most sporocytes at diakinesis and metaphase I but

TABLE 2. *Meiosis in diploid (2n = 14) plants of Festuca elatior.*

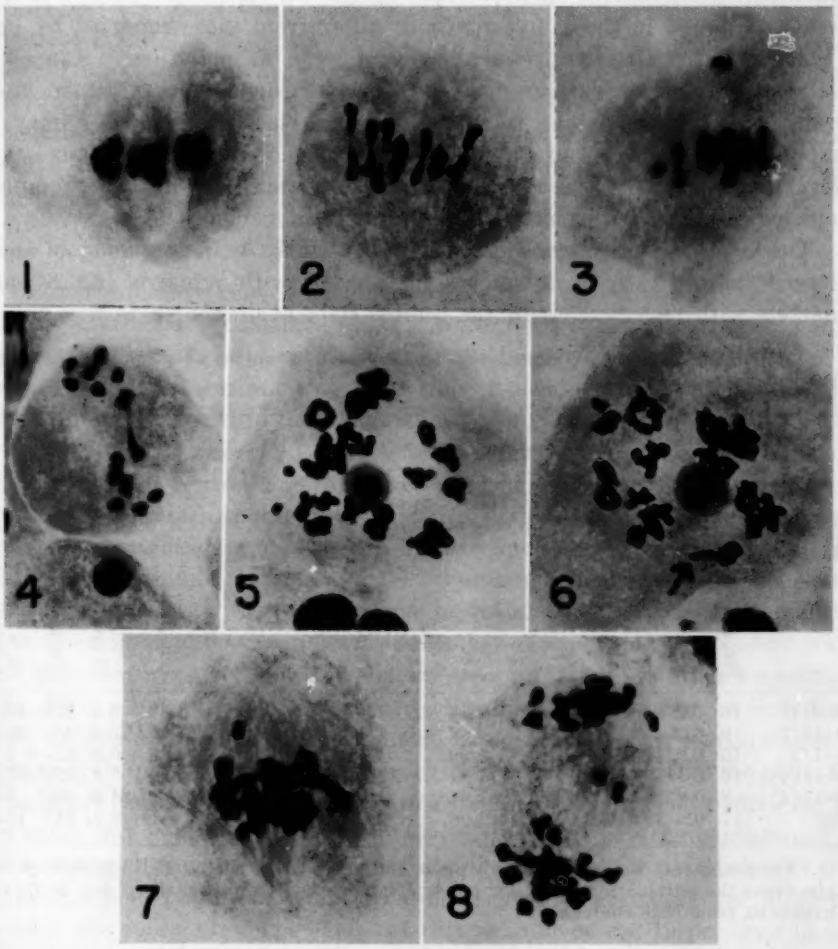
Plant No.	Diakinesis		Metaphase I		Anaphase I			Quartets	
						Per cent with			
	No. cells	X-ta per chromosome	No. cells	% with univalents	No. cells	Laggards	Bridge + fragment	No. cells	% with micronuclei
41–3(3)	20	1.76	209	7.2	126	0.8	2.4	226	3.5
41–130(5)	12	2.02	230	0.4	95	1.0	0.0	135	0.0
41–210(4)	12	2.04	142	5.6	108	5.6	0.0	111	0.9

occasional sporocytes were observed with six bivalents and two univalents (figs. 1, 2, 3). Likewise the incidence of lagging and equationally dividing univalents at anaphase I and of micronuclei in the quartets was relatively low. In these characteristics and also in chiasma frequency the plants were

[4] The authors are indebted to Mr. M. A. Hein, Senior Agronomist, Division of Forage Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Admin., U. S. Department of Agriculture, for this seed and for information of the origin of the varieties.

similar in behavior to diploid plants of *Lolium perenne* (Myers 1941). Dicentric chromatid bridges and acentric fragments were observed in one plant (fig. 4), indicating heterozygosity for an inversion in this plant.

At diakinesis in the six hexaploid plants (figs. 5, 6), the average frequency of bivalents per sporocyte ranged for the different plants from 16.2



FIGS. 1–8. Meiosis in diploid and hexaploid races of *Festuca elatior* L. × ca. 850. FIGS. 1, 2. Metaphase I in the diploid race with 7 bivalents. FIG. 3. Metaphase I in diploid race with 6 bivalents and 2 univalents. FIG. 4. Anaphase I in diploid race showing dicentric chromatid bridge. FIG. 5. Diakinesis in hexaploid race showing two unpaired centric fragments. FIG. 6. Diakinesis in hexaploid with two centric fragments associated by a single chiasma. FIG. 7. Metaphase I in hexaploid race showing paired but non-oriented centric fragments. FIG. 8. Anaphase I in hexaploid race with two lagging and dividing univalents.

to 19.8 while the average frequency of quadrivalents ranged from [illegible] to 2.8. The maximum number of quadrivalents in the sporocytes examined was 3 in 38–2(1), 4 in 38–12(2), 3 in 38–12(1), 5 in 38–1(1), 3 in 38–11(4), and 2 in 1407. Thus in no case was the theoretically possible maximum of seven quadrivalents observed. Sexivalents were observed in only one plant, 38–12(2), one sexivalent occurring in each of three of the six sporocytes analyzed. The results obtained in these investigations differ from those reported by Peto (1933) who found no multivalent association in *F. arundinacea* (2n = 42). Data on chromosome association in relation to homologies must be interpreted with caution since factors other than lack of homology may be responsible for absence of pairing, particularly of multivalent association. Nevertheless, there is no positive evidence from these data of complete homologies between chromosomes from different genomes.

The hexaploid plants varied considerably (table 3) in frequency of metaphase I sporocytes with univalents, anaphase I with laggards (fig. 8), and quartets with micronuclei. In the limited data available, there was no evi-

TABLE 3. *Chromosomal association and behavior in stages of meiosis in hexaploid plants of Festuca elatior.*

Plant No.	Diakinesis								Metaphase I		Anaphase I			Quartets	
	Average per sporocyte of					Half X-ta per chromosome in						% with			
	No. cells	I	II	IV	VI	II	IV	VI	Total	No. cells	% with univalents	No. cells	Laggards	Bridge + fragment	No. cells	% with micronuclei
38–2(1)	16	0.0	17.9	1.6	0.0	1.82	1.98	.....	1.84	214	10.3	90	14.4	3.3	172	16.3
38–12(2)	9	0.0	14.4	2.8	0.3	1.92	2.06	1.88	1.96	222	2.7	136	3.7	23.5	170	23.0[a]
38–1(1)	10	0.0	17.8	1.6	0.0	1.76	1.90	.....	1.78	203	4.9	14	14.3	0.0	221	7.7
38–12(1)	16	0.4	18.7	1.1	0.0	1.72	1.94	.....	1.74	130	11.6	37	59.4	5.4	120	17.4
38–11(4)	8	0.0	16.2	2.4	0.0	1.72	1.82	.....	1.76	203	1.0	64	4.7	21.9	160	4.4
1407	17	0.0	19.8	0.6	0.0	1.72	1.96	.....	1.74	124	2.4	164	6.1	9.2	167	17.8

[a] The fragments were large in this plant and often could not be distinguished at this stage from the chromatids from Anaphase I laggards. This value, therefore, is for all micronuclei from both sources.

dence that the irregularities of metaphase and anaphase were correlated with incidence of multivalents at diakinesis. In this regard, the results are consistent with those obtained previously in *Dactylis glomerata*, *Phleum pratense*, and autotetraploid *Lolium perenne* (Myers 1943, 1944, 1945; Myers & Hill 1942, 1943).

In five of the six plants, dicentric bridges and acentric fragments were observed in some sporocytes at anaphase I. In the sixth plant only 14 ana-

phase I sporocytes were examined. Such configurations ordinarily result from crossing-over in heterozygous inversions and have been found commonly in plants of naturally cross-pollinated, perennial grass species (cf. Myers, in press). The bridges and fragments in these plants may also have arisen from crossing-over in inverted segments of normally homologous chromosomes. On the other hand, some or all of these configurations could have resulted from structural rearrangements in partially homologous chromosomes from different genomes that paired occasionally to form quadrivalents or, rarely, sexivalents. In this regard, it is interesting, although perhaps only coincidental, that the two plants with high incidence of bridges and fragments [38–11(4) and 38–12(2)] also had the highest frequency of quadrivalents.

OCCURRENCE AND BEHAVIOR OF CENTRIC FRAGMENT CHROMOSOMES

Supernumerary centric fragments have been reported in diploid plants of *Festuca elatior* by Rancken (1934). Similarly, a centric fragment, in addition to the normal complement of 14 chromosomes, was found in four diploid plants of which chromosome numbers were determined in the present studies. Meiotic investigations in these plants have not yet been conducted.

In one of the hexaploid plants, 38–12(1), two fragments with approximately median centromeres were observed at diakinesis and metaphase I. In twelve of sixteen sporocytes at diakinesis, the two fragments were associated by a single chiasma (fig. 6). In two sporocytes, the fragments were paired with a single chiasma and the other arm of one fragment was associated by a chiasma with a chromosome in one of the bivalents. In one sporocyte, one fragment was paired with a member of a normal quadrivalent while the other was unpaired. Both fragments were unpaired in only one sporocyte (fig. 5). At metaphase I, two unpaired fragments were observed in 9.2 per cent of the 130 sporocytes examined, while a single unpaired fragment occurred in 0.8 per cent of the sporocytes. In 28.5 per cent of the cells, the fragments were paired but were not oriented on the equatorial plane (fig. 7). In many but not all of the remaining cells, the paired fragments could be seen among the bivalents and quadrivalents on the equatorial plane. At anaphase I, one or two lagging and dividing fragments were observed in 27 per cent of the sporocytes. The excess of this value over the 10 per cent of unpaired fragments at metaphase I may have resulted from lagging of part of the non-oriented fragment pairs. Observations of early anaphase I indicated that the oriented pairs of fragments disjoined and moved towards the poles along with the normal chromosomes.

Janaki Ammal (1939) postulated that the supernumerary chromosomes found in *Sorghum purpureo-sericeum* were relics of an evolutionary process of reduction in basic chromosome number. The fragment chromosomes of

Festuca elatior, because of their tendency to pair with normal chromosomes, could result, on the other hand, in the production of genetically balanced gametes of altered karyotype consisting of one chromosome more than normal. With proper conditions of isolation, therefore, the fragments of this species might provide an opportunity for evolutionary increase in basic chromosome number.

HYBRIDIZATION OF DIPLOID AND HEXAPLOID RACES

In the hybridization studies, advantage was taken of the facts that the plants used as parents were nearly completely self-sterile and that the F_1 plants could be identified readily and accurately by their intermediate chromosome number. Hence, emasculation of the female parent was unnecessary and crossing was effected by bagging together, just before flowering, panicles from diploid and hexaploid plants. Seed obtained in this manner was planted individually in pots and the chromosome numbers determined from root-tip preparations. Plants with 28 chromosomes were judged to be F_1 hybrids since no other 28 chromosome *Festuca* plants have been found in investigations at the U. S. Regional Pasture Laboratory.

A total of 13 panicles of as many hexaploid plants was cross-pollinated with panicles from diploid and 10 diploid panicles were crossed with hexaploid. Diploid panicles used in the other three cross-pollinations were not saved since they had started to flower before bagging. No F_1 plants were obtained when the hexaploids were used as the female parent. Similarly, none was obtained from seven of the diploid panicles used as females. From three diploid panicles, however, F_1 plants were found; eight from one, and one from each of the others. Less than half of the seed from each of the three panicles was used. Assuming an equal frequency of F_1 among the unused seeds, the total calculated number of F_1 obtained from the three panicles were 17, 3, and 2, respectively. Although the number of florets involved was not determined, the results suggest considerable variation in cross-compatibility of the different parent plants.

The variation between reciprocals in this investigation is consistent with the results reported by Jenkin (1933) in hybridization of *Lolium* with *Festuca* and by Nilsson (1939) in hybridization of *F. pratensis* (= *F. elatior*, $2n = 14$) × *F. arundinacea* (= *F. elatior* var. *arundinacea*, $2n = 42$). These crosses, likewise, were usually most successful when the female parent had the lower chromosome number. Such results are different from those most commonly obtained in interspecific hybridization (cf. Watkins 1932; Thompson 1930, 1940; Müntzing 1933).

Clones of the F_1 plants were grown in the greenhouse in the winters of 1944–45 and 1945–46. One clone flowered both winters and three others flowered during the second winter. The clones were completely male-sterile,

not a single anther dehiscing. Furthermore, no seed was obtained on more than 20 panicles that flowered in close proximity to dehiscing plants of diploid *F. elatior*.

MEIOSIS IN INTER-RACIAL AND INTERSPECIFIC HYBRIDS

Chromosomal behavior during meiosis was studied in one F_1 plant of *Festuca elatior* (2x) × *F. elatior* (6x) and in one F_1 plant of *Lolium perenne* × *F. elatior* (6x). As can be seen in table 4, pairing at diakinesis was essentially similar in the two plants. A majority of the chromosomes occurred

TABLE 4. *Chromosome pairing at diakinesis in F_1 hybrids of Lolium perenne × F. elatior (6x) and of F. elatior (2x) × F. elatior (6x).*

Plant No.	Diakinesis								
	No. cells	Average number of							Total x-ta
		I	II	X-ta[c]	III	X-ta	IV	X-ta	
1[a]	16	1.25	8.44	1.60	0.60	1.60	2.00	1.54	1.50
2[b]	9	1.33	7.78	1.78	0.89	1.50	2.11	1.68	1.64

[a] Plant Number 1—F_1 of *Lolium perenne* × hexaploid *Festuca elatior*.
[b] Plant Number 2—F_1 of diploid *F. elatior* × hexaploid *F. elatior*.
[c] Half-chiasmata per chromosome.

as bivalents, with some paired as quadrivalents and, less frequently, as trivalents or unpaired. The chiasma frequencies were somewhat lower than in the diploid or hexaploid plants examined, indicating some interference with pairing or chiasma formation in the hybrid plants, caused perhaps by partial lack of homology between the chromosomes that paired.

The high frequency of bivalents, trivalents and quadrivalents in these hybrid plants indicates, however, considerable homology between chromosomes of different genomes in the hexaploid and between chromosomes of the diploid and of the hexaploid. In this respect, the behavior is consistent with that observed in the hexaploid plants (table 3) where quadrivalents and, rarely, sexivalents occurred. The results agree fairly well with those reported by Peto (1933) for hybrids of *Lolium perenne* × *Festuca arundinacea* (*F. elatior* var. *arundinacea*). He found an average of 9.07 univalents, 7.73 bivalents, 0.40 trivalents, 0.40 quadrivalents, and 0.13 quinquevalents per sporocyte. In *F. pratensis* × *F. arundinacea* (*F. elatior*, 2x, × *F. elatior*, 6x), however, Nilsson (1939) reported that $7_{II} + 14_I$ were normally found in meiosis.

The similarity of chromosome pairing between *Lolium perenne* × *Festuca elatior* (6x) and *F. elatior* (2x) × *F. elatior* (6x) is of particular interest with respect to reported chromosomal behavior in F_1 plants of *L. perenne* × *F.*

elatior (2x). In these hybrids, Peto (1933) found 7 bivalents regularly formed with a chiasma frequency only slightly lower than that of the two parents, indicating rather complete homology between chromosomes of the two species. The present study provides further evidence of the similarities of the *Lolium* and *Festuca elatior* genomes so far as pairing relationships are concerned.

DISCUSSION

Cytogenetic studies of intraspecific chromosome races are of interest to the systematist, the cytogeneticist, and the plant breeder. Although determination of the taxonomic status of the diploid and hexaploid races was not within the scope of these investigations, certain of the results have considerable bearing on that problem. Under comparable and favorable conditions, such as in the plant breeding nursery and greenhouse, most plants of the two races are rather readily distinguishable by casual inspection. It seems probable that measurements of various plant organs would reveal significant and rather consistent size differences between plants of the races.

In the crossing experiments, F_1 seed and plants were obtained relatively infrequently even when compatible pollen of the female parent species was excluded. It is probable, therefore, that in nature F_1 hybrids would occur very rarely. Furthermore, results of these investigations indicate that the F_1 hybrid plants are nearly, if not quite, sterile. Hence, frequency of gene exchange between the two races, under natural conditions, would be extremely low. From these standpoints, the two races, with some justification, might be given specific rank as has been done in fact, by some European workers. From the standpoint also of their use as forage plants, there might be some justification for considering these races as different species. Many agronomists and plant breeders recognize that meadow and tall fescue are distinct crops, adapted to different conditions and uses.

The role of autopolyploidy in origin of new forms has been much debated. Müntzing (1936) summarized considerable information that seemed to provide evidence of the importance of autopolyploidy in this respect. The polyploid intraspecific chromosome races were considered by him to have arisen as autopolyploids and Darlington (1937) has expressed a similar opinion. The data from meiosis in the hexaploid *Festuca elatior* and in hybrids of hexaploid with diploid *F. elatior* and *Lolium perenne* indicate that this race does not behave cytologically as an autohexaploid at the present time. Pairing between chromosomes of the different genomes is not complete. Therefore, if the hexaploid race arose originally as an autohexaploid, the pairing relationships of its chromosomes evidently have been altered during the course of development since that time. On the other hand, meiotic pairing indicated considerable homology between chromosomes of the diploid and hexaploid

and between chromosomes of different genomes of the hexaploid. Thus if the hexaploid arose from chromosome doubling in a hybrid of two species, these putative parents must have been closely related and their genomes may have been derived from a common origin. The origin of the hexaploid cannot be postulated, therefore, with the evidence at hand.

The occasional pairing of chromosomes from different genomes, which results in quadrivalent and sexivalent formation, provides a mechanism of exchange of genes between genomes. Such exchanges would be expected only in homologous chromosome segments of sufficient length to permit chiasma formation and in the chromosome regions distal to such homologous segments. For genes located in the homologous regions, segregation ratios might be expected to be intermediate between the typical tetrasomic and the dihybrid ratios. When non-homologous regions occur distal to homologous regions, single crossovers in the homologous segments, followed by distribution of adjacent members of the quadrivalents to the poles in meiosis, might result in the production of non-viable gametic types because of deficiencies and duplications. Thus hexaploids of the chromosomal constitution indicated for *Festuca elatior* var. *arundinacea* might be expected to exhibit some sterility directly attributable to formation and disjunction of the multivalent associations.

Sterility of F_1 hybrids between diploid and hexaploid races of *F. elatior* seriously handicaps efforts to transfer characters from one race to the other. It is possible, however, that more extensive investigations might reveal sufficient fertility to allow for such a transfer. Because of the low incidence of crossing and the sterility of the F_1 hybrids, it is evident that the two races may be handled as separate crops in production of foundation, registered, and certified seed of superior varieties. They may be grown in close proximity without danger of intercrossing.

SUMMARY

In *Festuca elatior* L., plants of the meadow fescue type regularly had $2n = 14$ chromosomes while plants of the tall fescue type, *F. elatior* var. *arundinacea* (Schreb.) Wimm., had $2n = 42$. Both types occurred in natural stands in central Pennsylvania but the diploid was considerably more common.

Meiosis in the diploid was regular while in the hexaploid there were found quadrivalents and, rarely, sexivalents at diakinesis, univalents at metaphase I, laggards at anaphase I and micronuclei in the quartets. Evidence of considerable homology between chromosomes of the diploid and hexaploid races and between chromosomes of different genomes of the hexaploid was provided by the high incidence of pairing at meiosis in F_1 hybrids.

In controlled cross-pollinations between diploid and hexaploid types, few

F_1 seeds were obtained and the hybrid plants were both male and female sterile.

UNITED STATES REGIONAL PASTURE RESEARCH LABORATORY
STATE COLLEGE, PENNSYLVANIA

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SECONDARY ROOT STIMULATION IN THE COMMON BEAN, PHASEOLUS VULGARIS L., CAUSED BY THE INSECTICIDES DDT AND COLORADO 9[1]

JESS L. FULTS AND MERLE G. PAYNE[2]

Although much information has been published concerning the use of DDT as an insecticide, very little is known concerning its effects on plants. Two exceptions to this are the work of Appleman and Sears (1) and Payne and Fults (3) who have reported on the depressing effect of DDT on root nodule formation in legumes.

During the progress of these studies the authors observed secondary root stimulation in a few plants which had been grown in soil treated with a high

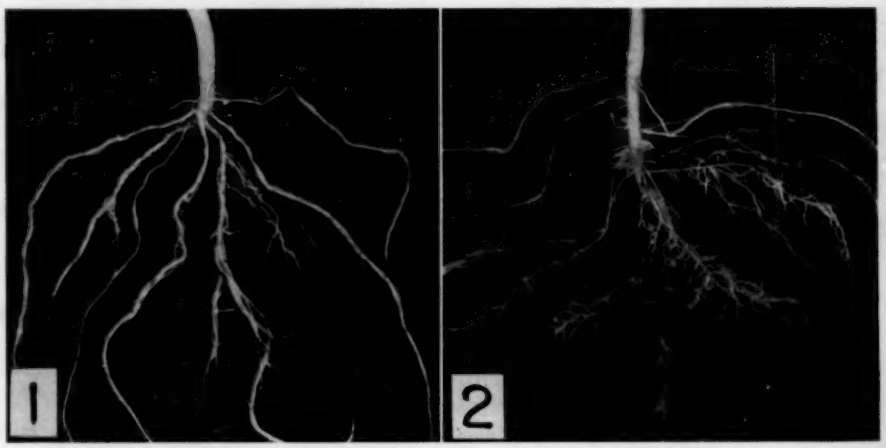

FIG. 1. Part of the root system of a water control plant of a common bean. Note the number of secondary roots arising from the main laterals. FIG. 2. Part of the root system of a plant of a common bean grown in soil treated with the insecticide DDT, at a high rate of application (127 p.p.m.). Note the increased number of secondary roots on the main laterals.

concentration of DDT. In order to evaluate the significance of this observation, a replicated test of the effects of both DDT and the new insecticide Colorado 9 (2) was made.

[1] 1-trichloro-2,2-bis-(p-chlorophenyl)ethane (DDT) and 1-trichloro-2,2-bis-(p-bromophenyl)ethane (Colorado 9).

[2] Associate botanist and associate chemist, respectively. Published with the approval of the Director of the Colorado Agricultural Experiment Station as Scientific Series Paper No. 226. The authors are grateful to Andrew G. Clark, Professor of Mathematics, Colorado A. & M. College, for his counsel in connection with the statistical analysis.

MATERIALS AND METHODS

The two chemicals used were made in the laboratories of the Chemistry Section of the Colorado Agricultural Experiment Station as previously described (3). The plant tests were made between January 16 and February 8, 1946, in the greenhouses of the Botany and Plant Pathology Section. Both chemicals were added to the soil (one part sand and three parts clay loam) before planting. This was accomplished by spraying 15 ml. of a chemical emulsion on the surface soil of 6-inch clay pots and allowing it to dry. After drying, the soil from each pot was emptied on a clean sheet of paper, thoroughly mixed, and replaced; then seed was planted. Five pots, each containing five plants, were used for each of the two chemicals and for the water checks. The amount of chemical used was equivalent to 127 p.p.m. of soil or 103 pounds per acre. At the time of harvest, plants were removed from the pots and the soil was removed from their roots with a fine water spray. Data on numbers of secondary roots were obtained by floating the entire root system on a sheet of glass ruled into 1-inch squares. Since the characters of the root systems of all five plants in each pot treated with a given chemical appeared similar, quantitative data from only one plant per pot were obtained. Within each plant, three lateral roots were selected and the total number of secondary roots arising from a random 6-inch length were counted.

TABLE 1. *Analysis of variance of the effect of DDT, Colorado 9, and water on the numbers of secondary roots per 6-inch length of lateral root in the common bean.*

Variability due to	D/F	Sum of squares	Mean square (variance)	F-value	Required F	
					0.05	0.01
Treatments	2	8,945.90	4,472.95	20.44	3.22	5.15
Within treatments (error)	42	9,191.34	218.84	.....	.....	.....
Total	44	18,137.34	.....	.....	.....	.....

Comparison of treatment means by the "t" test

Treatment	DDT	Colorado 9	Water	Difference between means required for significance	
				0.05	0.01
	Secondary roots	Secondary roots	Secondary roots		
Means	65.50	31.33	52.2	10.9	14.6

Comparison	Difference in means	Significance
DDT and Colorado 9	24.27	$P > 0.01$
DDT and water	13.40	$P > 0.05$
Colorado 9 and water	20.87	$P > 0.01$

RESULTS AND DISCUSSION

An analysis of variance of the data on the effect of DDT, Colorado 9, and water on the number of secondary roots is presented in table 1. These data show a highly significant F value, and hence the "t" test for minimum significant mean differences was made as shown in the second half of table 1. These results show that treatment with DDT resulted in significantly more secondary roots and with Colorado 9 in significantly fewer than were present in control plants (see figures 1 and 2). None of the treated plants in these tests showed injurious effects in the tops.

Further studies are needed to determine whether or not DDT may be used at high concentrations in the soil to increase the extent of plant root systems under field conditions. Such increased root systems might result in accelerated moisture and nutrient absorption and top growth.

DEPARTMENT OF BOTANY AND PLANT PATHOLOGY AND
DEPARTMENT OF CHEMISTRY, COLORADO AGRICULTURAL
EXPERIMENT STATION
FORT COLLINS, COLORADO

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BULLETIN OF THE TORREY BOTANICAL CLUB
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CROWN GALL DISEASE ON RHUBARB

MICHAEL LEVINE

It is well known that plant tumors can be induced experimentally on many varieties of garden and house plants. The spontaneous development of this disease on garden plants, however, is not of usual occurrence. The sporadic development of crown gall on rhubarb (*Rheum rhaponticum*) grown commercially is of economic interest, as the fate of the crop might be in question. As far as it is known, crown gall on the rhubarb plant has hitherto been unmentioned in the literature. Smith and his colleagues (1911), in their description of the crown gall disease, give a long list of plants tested with *B. tumefaciens*, but fail to mention this species. Inoculations with the crown gall organism made in this laboratory on the petioles of young and mature leaves failed to elicit crown galls. The same response was obtained to treatment with α-naphthalene acetic acid. Necrotic areas were formed at the site of inoculation even though the stimulation of an active growth substance was added.

Recently Professor E. F. Guba sent the writer several specimens of rhubarb roots that consisted of large tumorous masses (fig. 1) apparently attached to or growing from the crown of the plant. Healthy-looking, pinkish-colored buds were also present. Another specimen which followed consisted of a root surrounded by a well formed tumor, as shown in figures 5 and 6. These plant tumors were diagnosed as crown gall; the evidence is pointed out below. The history of the rhubarb culture which yielded these plants appears of interest, for it seems to throw some light on rhubarb culture as well as the crown gall disease. The rhubarb stock known as the "Linnaeus" or "strawberry" variety on which these crown galls appeared, was traced back to 1892. The roots that revealed the crown galls had been growing on the same plot for 15–18 years. In 1945, while the roots were being removed to another farm, an estimated 10 per cent of the stock was found to have these tumorous masses. The purchaser, who saw these galls, refused to take more than half of the crop. The owner, who contended that the galls were of no significance, based his beliefs on the productivity of the stock. This is an interesting point as it relates to the biology of the crown gall on rhubarb and its economic significance.

A number of roots with large crown galls, together with six roots obviously free from the disease, were shipped to this laboratory, where they were set out in a suitable plot in early March, 1946. Figure 7 shows the plot of rhubarb plants fully grown at the end of July. Not a single plant failed to

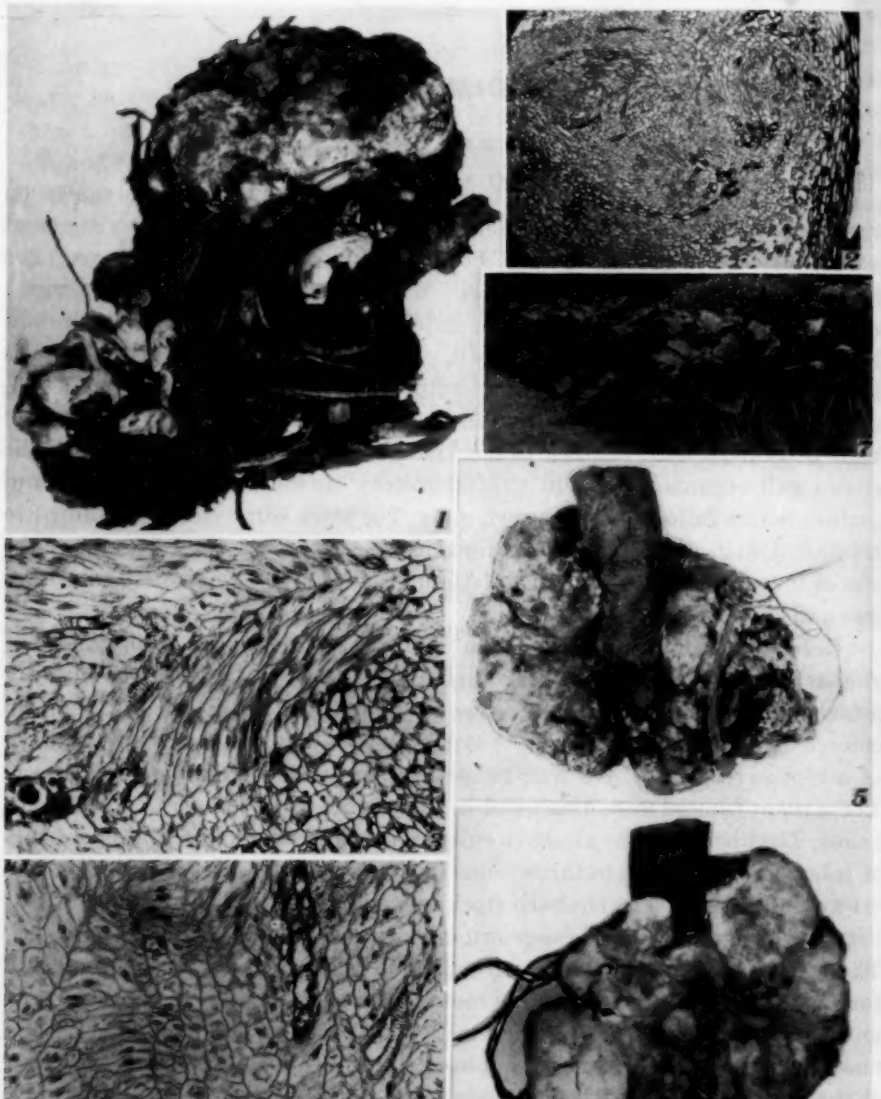

FIG. 1. Root of rhubarb with spontaneous crown gall and developing young leaf buds. ×0.5. FIG. 2. Section of a nodule of the crown gall shown in figure 1. ×120. FIGS. 3, 4. Sections of the gall under higher magnification showing characteristic crown gall tissue. ×240. FIG. 5. Root of rhubarb with surrounding crown gall. ×0.5. FIG. 6. Gross section through gall shown in figure 5. ×0.5. FIG. 7. View of plot in August in which crown-gall-infected and normal roots were planted early in March.

develop a large number of good sturdy leaves with thick succulent petioles. There is no difference between the size and number of leaves of the crown-gall-infected plants and of those without the galls. The fate of the old galls and the development of new galls were under observation. It is clear at this time that the old galls disintegrate. After several plants were dug up early in August, only the decomposed remains of the galls were found. The crowns and roots of the current year's growth appear normal and at this time no crown galls are present. Reinfection of the plant may have been arrested by lack of hoeing or harvesting. The common practice of plucking the leaves may be conducive to infection of the crown.

These observations confirm the studies previously made on experimentally induced crown galls on other garden plants. This overgrowth is not a malignant disease (Levine 1931) in the same category with induced or spontaneous neoplasia of animal or man. The growth appears to be a protective mechanism of limited proliferative capacity. The growth, unlike cancer, matures, grows old, and dies. In successive stages it finally becomes a corky, woody mass of tissue which disintegrates in the soil at the end of the season's growth. In perennial plants the gall above the soil becomes infested with saprophytic growths or dries and breaks off from the branch bearing it. Occasionally on trees and bushes such as the rose reinfection occurs. The old woody gall of the previous season becomes displaced by new growth.

The rhubarb galls of the current year begin to disintegrate in the late fall and the new active roots and crowns may become infected as the result of plucking the leaves. In the spring the leaf buds at the crown develop rapidly and give all appearances of healthy plants. The newly formed galls develop more slowly and do not interfere with the new growth of the leaves. It seems that the commercial product is entirely unaffected. This is borne out by the observations of the grower who only discovered the presence of crown gall disease when the plants were uprooted after twelve years of growth. What effect this disease has on the number of available healthy clones has not been determined. The roots used for propagation purposes could be infected with the crown gall organism at planting time.

The crown gall on the rhubarb plant is a white mass of tissue covered by a heavily mottled brownish-colored coat. The inner structure of a fully formed gall is of a white, firm, fibrous texture (fig. 6). In old galls gathered in November numerous areas of necrosis are seen (fig. 8) on the periphery. At this period many of the galls are in the process of disintegration.

On microscopic examination the fresh gall reveals the characteristic crown gall structure. Figure 2 represents a section through a large smooth nodule on the surface of the main gall shown in figure 1. The parenchymatous cells are small with many crystal-like inclusions. A disoriented array of tracheids and vessels runs through the body of the overgrowth. Under

higher magnification (figs. 3, 4) nucleated protoxylem cells appear in clusters. Few cells were found in division, although the overgrowth was viable, and no evidence of degeneration was present.

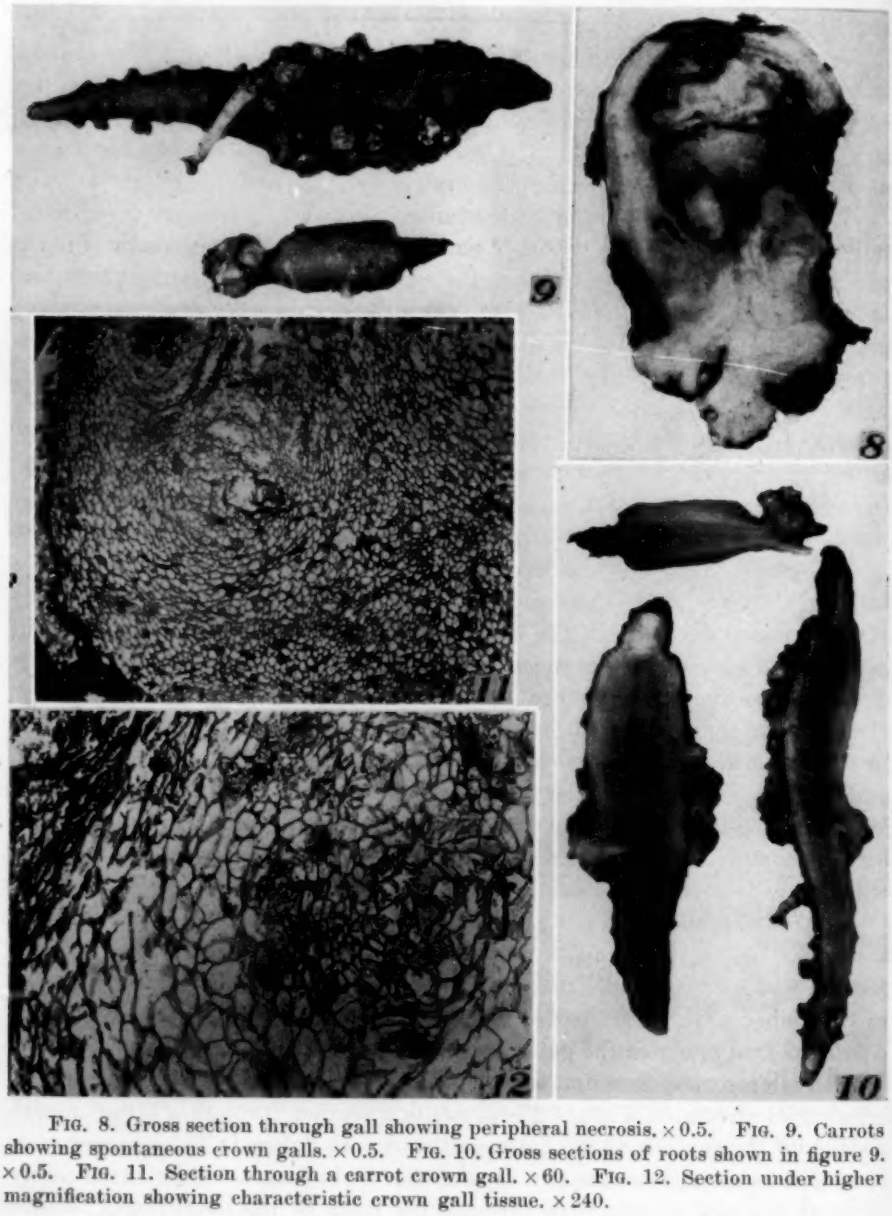

FIG. 8. Gross section through gall showing peripheral necrosis. × 0.5. FIG. 9. Carrots showing spontaneous crown galls. × 0.5. FIG. 10. Gross sections of roots shown in figure 9. × 0.5. FIG. 11. Section through a carrot crown gall. × 60. FIG. 12. Section under higher magnification showing characteristic crown gall tissue. × 240.

Attempts to isolate the causative organism yielded a rod-shaped schizomycete. Its cultural characteristics were unmistakably similar to those of *B. tumefaciens*. Smears, however, revealed rods with slime in greater abundance than is usually observed on the crown gall organism. The measurements were slightly larger than those of the tumor-producing bacteria. A small number of potted plants were inoculated with the organism but no crown galls larger than well developed scars resulted.

Rhubarb crown gall is another plant tumor that shows all the gross and microscopical morphological characteritstics of crown galls spontaneously or artificially induced. It perpetuates itself from year to year by infecting through the soil injuries induced by propagation. Its effect on the crop of leaves produced in a season is apparently slight as observed over a period of 15–18 years by competent growers.

While this work was in progress, another spontaneously developed gall on the carrot, *Daucus carota*, was brought to this laboratory for identification. The specimens were comparatively small and the root lines were covered with small nodules (figs. 9, 10) not unlike crown galls in appearance. In the photograph of the smaller specimen the tip of the root terminates in a large gall. Microscopic sections of these tumors revealed an abundance of hyperplastic parenchymatous cells (figs. 11, 12) with nodules of scalariform tubes. Little or no hypertrophy was present. The presence of these elements confirmed the diagnosis of crown gall in spite of the fact that some few sections showed nematode invasion of this tissue. Cultural studies of the gall yielded a rod-shaped bacterium which when grown on bean agar had all the characteristics of *B. tumefaciens*. Smears of the organism appeared identical with virulent cultures of *B. tumefaciens*. Inoculations with the organisms, however, produced small crown galls on *Ricinus* grown in the field. Potted plants grown in the laboratory were only slightly reactive to the inoculation with this organism.

SUMMARY

Rhubarb is apparently a new host for the crown gall disease. It occurs on the crown and roots of the plant. The petioles of rhubarb leaves inoculated with the crown gall organism produce no tumors. Spontaneous overgrowths on the garden carrot are typical crown galls produced by a tumor-producing schizomycete. Secondary nematode infection of the crown gall tissue is reported.

LABORATORY DIVISION, MONTEFIORE HOSPITAL
NEW YORK

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Postscript. On October 17, 1946, all the rhubarb plants were up-rooted for the purpose of ascertaining the number of crown galls, if any, that may have been formed during the growing season. Only one plant produced a large pedunculate crown gall. The tumor was the size of a large grapefruit and was attached to the lower surface of the crown by a short, stubby stalk. The gall was soft and necrotic, and disintegrated on pressure. The rest of the plant was sound and produced a number of leaves equal to that of the other plants. Sixty pounds of marketable petioles and only one gall were produced by the crown-gall-bearing plants set out in March. How infection occurred in this plant is not clear. A moderate number of leaves were plucked throughout the season from all plants. The inoculations made in the petioles produced no tumors.

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STUDIES ON PHILIPPINE CHLOROPHYCEAE— III. THE CODIACEAE

WILLIAM J. GILBERT

The earliest published record of a species of the Codiaceae from the Philippines is *Fucus prolifer* Blanco, which appeared in the first edition of Blanco's *Flora de Filipinas* (1837, p. 838). The description refers to a species of *Halimeda* and may be applied to any one of several species in that area. A few years later Berkeley (1842, p. 157), using the name *Dichonema erectum*, described what he thought to be a fungus but which A. Gepp and E. S. Gepp later showed to be an alga, since known as *Avrainvillea erecta* (Berkeley) A. & E. S. Gepp. Following this, papers mentioning the Codiaceae are few and scattered, the more important being Martens (1866), Dickie (1876), and Weber-van Bosse (1913). More recent papers dealing at all with Philippine Chlorophyceae have contained no records of the Codiaceae except for the description of two new species of *Codium* from the South China Sea (Tseng & Gilbert 1942).

Sources of material for this study are those mentioned previously by the writer (1942, 1943) with the addition of two smaller collections. Of these latter one was made in 1937 by Dr. José V. Santos at Puerto Princesa, Palawan, and the other by Dr. Gregorio T. Velasquez in the vicinity of Puerto Galera, Mindoro. As in most collections of tropical marine algae, members of the Codiaceae, especially of *Halimeda*, were abundant.

Twenty-three species of Philippine Codiaceae are discussed in the following pages. No attempt has been made to include species which have been reported heretofore from the Philippines but which are not found in the collections studied. These are few, however, and only two have come to the attention of the writer which do not resolve into synonomy with some species on the following pages. One of these is *Halimeda cuneata* Kützing (not *H. cuneata* Hering) reported by Martens (1866, p. 25) and which is now considered to be *Halimeda gracilis* Harvey. The second is the report of *Codium tomentosum* (Hudson) Stackhouse by Dickie (1876, p. 243), now known as *C. dichotomum* (Hudson) S. F. Gray. Geographically both of these species may be expected in this area.

Of the twenty-three species listed eleven appear to be new records for the Philippines, with two genera, *Chlorodesmis* and *Tydemania*, reported for the first time. The new records include *Chlorodesmis comosa, C. Hildebrandtii, C. formosana, Tydemania expeditionis, Udotea javensis, Codium coronatum, C. Geppii, C. contractum, C. intricatum, Halimeda orientalis,* and *H. Monile.*

CHLORODESMIS Bailey & Harvey

CHLORODESMIS COMOSA Bailey & Harvey, 1851, p. 373; A. & E. S. Gepp, 1911, p. 14, *pl. 8, f. 69–73.*

Collections: *Merrill 9161,* Taytay, Palawan, May; *Ebalo A–30,* Punta Mangal, Basilan Island, Jan.; *Bartlett A–91,* near Philippine Desiccated Coconut Factory, Zamboanga, Jan.–Feb.; *Balhani 159,* Lanhil (Little Sibago) Island, Jan.–Feb.; *873,* Saluping Island, due S. of Cabengbeng, Basilan Island, Jan.–Feb.

CHLORODESMIS HILDEBRANDTII A. & E. S. Gepp, 1911, p. 16, 137, *pl. 8, f. 74, 75a, pl. 9, f. 75b;* Tseng, 1936, p. 163, *f. 22.* Collections: *Bartlett 15001, 15033,* Dalupiri Island, Babuyan Group, Oct.–Nov.

The range of diameters of the ascending filaments in the material at hand is somewhat less than the 80–130 μ called for by the original description. A few of the filaments reach a diameter of 115 μ.

CHLORODESMIS FORMOSANA Yamada, 1925, p. 92, *f. 5;* Okamura, 1930, p. 104. Collection: *Bartlett 15034,* Dalupiri Island, Babuyan Group, Oct.–Nov.

AVRAINVILLEA Decaisne

AVRAINVILLEA ERECTA (Berkeley) A. & E. S. Gepp, 1911, p. 29, *pl. 9, f. 84, 85; pl. 10, f. 86–89. Dichonema erectum* Berkeley, 1842, p. 157, *pl. 7, f. 11;* Collections: *Santos 658,* Buenavista, Puerto Princesa, Palawan, April; *Balhani 699,* Kilay (Langasmati) Island, near Langas Island, off the W. coast of Basilan Island, Jan.–Feb.

TYDEMANIA Weber-van Bosse

TYDEMANIA EXPEDITIONIS Weber-van Bosse, 1901, p. 139; 1913, p. 116; A. & E. S. Gepp, 1911, p. 66, *f. 153, 154; Rudicularia penicillata* Heydrich, 1903, p. 97, *f. 1–4.*

Collections: *Bartlett 13988,* Puerto Galera, Mindoro, May; *Velasquez 777,* Paniquian Island, near Puerto Galera, Mindoro, April; *989,* Northwest Channel, Medio Island, near Puerto Galera, Mindoro, April; *1066,* Boaya Point, vicinity of Puerto Galera, Mindoro, April; *Bartlett 16039,* Siasi Island, Sulu Archipelago, Sept.

The known range of *Tydemania expeditionis* has been considerably extended since its discovery in the Siboga material and subsequent description, for it has since been reported from the Indian Ocean, Caroline and Liu-kiu[1] Islands, and now from the Philippines.

UDOTEA Lamouroux

UDOTEA JAVENSIS (Montagne) A. & E. S. Gepp, 1904, p. 363, *pl. 467, f. 1–4;* 1911, p. 110, *pl. 5, f. 36; Rhipidosiphon javensis* Montagne, 1842, p. 14. Collections: *Merrill 9140 p.p.,* Taytay, Palawan, April; *Ebalo A-11a,* Tumakid, Basilan Island, Jan.

UDOTEA ORIENTALIS A. & E. S. Gepp, 1911, p. 119, *f. 1, 4, 47, 48;* Weber-van Bosse, 1913, p. 117; Yamada, 1934, p. 74, *f. 42, 43. Udotea conglutinata* Okamura (not Lamouroux), 1908, 1(9): 231, *pl. 44, f. 11, 12, pl. 45, f. 8–13.*

[1] Liu-kiu is the spelling used for that group of islands known also as Riu-kiu, Ryukyu, Lu-chu, or Loochoo Islands.

Collections: *Bartlett 14609*, Dalupiri Island, Babuyan Group, July; *15024*, Dalupiri Island, Babuyan Group, Oct.–Nov.; *14145*, Santa Cruz, Zambales Province, Luzon, May; *Merrill 9140 p.p.*, Taytay, Palawan, April.

UDOTEA ARGENTEA Zanardini var. SPUMOSA A. & E. S. Gepp, 1911, p. 126, *pl. 2, f. 15, pl. 3, f. 25a, pl. 7, f. 61, 62;* Weber-van Bosse, 1913, p. 117. Collections: *Bartlett 15587*, small island opposite Culion Harbor, Culion Island, Calamian Group, July; *Merrill 9149*, Taytay, Palawan, April.

UDOTEA FLABELLUM (Ellis & Solander) Lamouroux, 1812, p. 186; *Corallina Flabellum* Ellis & Solander, 1786, p. 124, *pl. 24; U. Flabellum* Howe, 1904, p. 94. Collection: *Bartlett A-199*, Little Santa Cruz Island, opposite Zamboanga, Jan.–Feb.

CODIUM Stackhouse

CODIUM ADHAERENS (Cabrera) C. Agardh, 1822, p. 457; *Agardhia adhaerens* Cabrera (ms.) in Phys. Sällsk. Årsber (quoted from De Toni, 1889, p. 489). Collection: *Bartlett 13788*, Puerta Galera Bay, Puerto Galera, Mindoro, May.

CODIUM CORONATUM Setchell, 1926, p. 82, *pl. 10, f. 2–5, pl. 11, f. 2, 3, pl. 12, f. 1, 5;* Børgesen, 1936, p. 67; Tseng, 1938, p. 148.

Collections: *Velasquez 753*, Balatero Maliit, vicinity of Puerto Galera, Mindoro, April; *825, 1017*, Balete, Varadero Bay, near Puerto Galera, Mindoro, April; *878*, Balatero Malaki, near Puerto Galera, Mindoro, April; *1074*, Ensanada, vicinity of Puerto Galera, Mindoro, April; *Bartlett 13953*, Puerto Galera Bay, Puerto Galera, Mindoro, May; *14016*, Batangas Channel, Puerto Galera, Mindoro, May; *Merrill 9146*, Taytay, Palawan, April; *Santos 656*, Buenavista, Puerto Princesa, Palawan, April; *Balhani 655*, Sibakel Island, Zamboanga Province, Jan.–Feb.; *681*, Tengolan Island (W. of Malusa Bay, Basilan Island), Jan.–Feb.

CODIUM GEPPII Schmidt, 1923, p. 50, *f. 33; C. divaricatum* A. & E. S. Gepp, 1911, p. 145; Weber-van Bosse, 1913, p. 119.

Collections: *Bartlett 16238*, Dalupiri Island, Babuyan Group, July; *Fénix, Bureau of Science no. 13079*, San Fernando, La Union Province, Luzon, Feb.; *Velasquez 1018*, Balete, Varadero Bay, near Puerto Galera, Mindoro, April; *1063*, Boaya Point, vicinity of Puerto Galera, Mindoro, April; *Bartlett 13789, 13997*, Puerto Galera, Mindoro, May.

CODIUM INTRICATUM Okamura, 1913, **3**(4): 74, *pl. 120, f. 9–13;* Schmidt, 1923, p. 55; Yamada, 1934, p. 79; Tseng, 1936, p. 169, *f. 26c.* Collection: *Balhani 590*, Sikeang, S. W. of Punta Matangal, E. coast of Basilan Island, Jan.–Feb.

It is with some hesitation that this specimen is assigned here because the utricles measure but 115–255 μ in diameter and thus do not begin to approach the measurements (770–1150 μ diameter) of the original description. But since the external morphology of the plant as well as the shape of the utricles agree so well with Okamura's original description it is felt that it can best be placed here. Yamada (1934, p. 79) and later Tseng (1936, p. 170) have both referred to this species plants with utricles not much larger than in the material at hand.

CODIUM BARTLETTII Tseng & Gilbert, 1942, p. 291, *f. 1, 2a.*

Collections: *Velasquez 754*, Balatero Maliit, vicinity of Puerto Galera, Mindoro, April; *809*, Hondura Bay, near Puerto Galera, Mindoro, April; *879*, Balatero Malaki, vicinity of Puerto Galera, Mindoro, April; *993*, Paniquian Island, vicinity of Puerto Galera, April; *1046*, Sabang, near Puerto Galera, Mindoro, April; *Bartlett 13954*, Puerto Galera Bay, Puerto Galera, Mindoro, May; *14015*, Batangas Channel, Puerto Galera, Mindoro, May.

CODIUM CONTRACTUM Kjellman, 1897, p. 35, *pl. 2, f. 12, pl. 7, f. 1–3;* Okamura, 1913, **3**(4) : 70, *pl. 120, f. 1–8;* Schmidt, 1923, p. 57, *f. 38, 39.* Collection: *Bartlett 14595*, Cavite, Cavite Province, Luzon, July.

CODIUM PAPILLATUM Tseng & Gilbert, 1942, p. 293, *f. 2b–d, 3.* Collections: *Bartlett 14595a*, Cavite, Cavite Province, Luzon, July; *Shaw 1146*, Lamao, Province of Bataan, Luzon, May; *Bartlett 13786*, Puerto Galera Bay, Puerto Galera, Mindoro, May.

CODIUM sp. *Balhani 631*, Panigayan Islands, W. of Isabela de Basilan, Jan.–Feb.

This is a fragmentary specimen, apparently of erect growth, in which the segments are cylindrical, 3–4 mm. broad, and here and there attached to one another by tufts of rhizoidal filaments. The plant is sterile. The utricles are clavate to pyriform, or obovoid, 330–540 μ broad and 710–850 μ long, and have rounded or truncate apices. The size and shape of the utricles agree well with *Codium Mülleri* Kützing, which may be expected in this region, but that species does not appear to have the segments connected by tenacula, nor does the material at hand have the much thickened apical wall characteristic of the utricles of *C. Mülleri*. It seems quite likely that the plant has not been described but it cannot be treated satisfactorily in its fragmentary and sterile condition.

HALIMEDA Lamouroux

HALIMEDA TUNA (Ellis & Solander) Lamouroux f. TYPICA Barton, 1901, p. 13, *pl. 1, f. 1.* This form is characterized by segments that are reniform, discoid, or transversely oblong, the segments reaching 2 cm. broad and 1.2 cm. high.

Collections: *Bartlett 14954*, Currimao, Ilocos Norte Province, Luzon, Oct.; *Williams, R. S.* Daron, Mindanao, March; *Bartlett 16158*, Little Santa Cruz Island, Basilan Strait, Zamboanga, Mindanao, Sept.; *Balhani 309*, Bilang-bilang, near Moro Community, Zamboanga Province, Jan.–Feb.; *750*, Boboh, near Punta Matangal, E. point of Basilan Island, Jan.–Feb.

HALIMEDA TUNA f. *platydisca* (Decaisne) Barton, 1901, p. 14, *pl. 1, f. 2; H. platydisca* Decaisne, 1842, p. 102. The segments are larger than in the form above, reaching 3.4 cm. in width and 2.5 cm. in height, and are reniform, discoid, or transversely ovoid.

Collections: *Velasquez 835*, Paniquian Island, vicinity of Puerto Galera, Mindoro, April; *990*, Northwest Channel, Paniquian Island, vicinity of Puerto Galera, Mindoro, April; *864*, east shore of Muelle, vicinity of Puerto Galera, Mindoro, April; *Bartlett 13934, 13991*, Puerto Galera, Mindoro, May; *15585*, small island opposite Culion Harbor, Culion Island, Calamian Group, July; *Ebalo A–7, A–25*, Basilan Island, Jan.; *Balhani 338, 523, 612, 793, 804, 827*, Basilan Island, Jan.–Feb.; *653*, Sibakel Island, Zamboanga

Province, Jan.–Feb.; *698*, Kilay (Langasmati) Island, near Langas Island off the W. coast of Basilan Island, Jan.–Feb.; *817*, Kauluan Island off the S. E. coast of Basilan Island, Jan.–Feb.; *Bartlett 16034*, Siasi Island, Sulu Archipelago, Sept.

HALIMEDA DISCOIDEA Decaisne f. TYPICA Howe ex Børgesen, 1911, p. 134. The segments are discoid, obovate, or somewhat cuneate, in general wider than their length.

Collections: *Bartlett 14618*, Dalupiri Island, Babuyan Group, July; *Velasquez 986*, San Isidio, vicinity of Puerto Galera, Mindoro, April; *Balhani 177*, Pangapuyon Island, Zamboanga Province, Jan.–Feb.; *274*, Sangali, near Bolong, 19 miles N. N. E. of Zamboanga, Jan.–Feb.; *324*, Balas, near Lamitan, N. E. coast of Basilan Island, Jan.–Feb.

HALIMEDA DISCOIDEA f. **subdigitata** Gilbert, f. nov. Planta usque ad 18 cm. alta, articulis inferioribus late cuneatis, superioribus anguste cuneatis vel digitatis.

TYPUS: *H. H. Bartlett 16036*, ex Siasi Island, Sulu Archipelago, Insulis Philippinis, 15 IX 1935, in Herb. Univ. Michiganensi.

This form of *Halimeda discoidea* reaches 18 cm. in height, and differs from the typical form by having the lower segments broadly cuneate, and those above narrowly cuneate to finger-like. From the top of some of the broader segments originate 3–8 segments digitately.

Collections: *Velasquez 824*, Varadero Bay, vicinity of Puerto Galera, Mindoro, April; *1023*, San Teodora Municipality, near Puerto Galera, Mindoro, April; *Merrill 9147*, Taytay, Palawan, April; *Bartlett A–89*, near Philippine Desiccated Coconut Factory, Zamboanga, Jan.–Feb.; *A–197*, Little Santa Cruz Island, opposite Zamboanga, Jan.–Feb.; *Balhani 124*, Sibago Island (at E. entrance to Strait of Basilan), Jan.–Feb.; *141*, Tabtabon (Tictavon) Island, S. E. of Zamboanga, Jan.–Feb.; *157*, Lanhil (Little Sibago) Island, Jan.–Feb.; *310*, Bilang-bilang, near Moro Community, Zamboanga Province, Jan.–Feb.; *426*, Labuan, 20 miles N. W. of Zamboanga, Jan.–Feb.; *470*, Bavara, Pangapuyan (Pangapuan) Island, Zamboanga Province, Jan.–Feb.; *872*, Saluping (Salipin) Island, due S. of Cabengbeng, Basilan Island, Jan.–Feb.; *Bartlett 16036*, TYPE, Siasi Island, Sulu Archipelago, Sept.

Because the external morphology of this and the following form so strongly suggests *Halimeda cuneata* Hering forms *digitata* Barton and *typica* Barton some explanation is required. For some time many of the plants listed above under *H. discoidea* were considered to be representatives of *H. cuneata*. The writer was influenced primarily by the similarity in form between these plants and the figures presented by Barton (1901, p. 16, *pl. 2, f. 7, 9*) for the aforementioned forms of *H. cuneata*. The relative ease with which the fused nodal filaments were separable upon decalcification and the somewhat greater diameter of the cortical utricles than is usual in *H. cuneata* suggested doubt concerning the validity of the determinations. A closer microscopical examination then revealed that every specimen on hand possessed the large, bullate, subcortical utricles which are characteristic only of *H. discoidea* to which Howe (1907, p. 496) first called attention. Some of the subcortical utricles reach 200 μ in diameter and they always appear much larger than the 6–14 cortical utricles borne on them. The large size of the subcortical utricles, the relative ease of separation of the fused nodal filaments, the relatively large subquadrate cortical utricles, and the absence of

a cushion-like base to the segments indicated that the plants were specimens of *Halimeda discoidea* and not *H. cuneata*.[2]

Inasmuch as Barton (1901) made no mention of subcortical utricles in her outstanding monograph of the genus *Halimeda*, there is a real possibility that all or part of the plants she designated as *H. cuneata* f. *digitata* may be *H. discoidea* f. *subdigitata*. Likewise, part of the plants she considered *H. cuneata* f. *typica* may be the following form of *H. discoidea*.

HALIMEDA DISCOIDEA f. **intermedia** Gilbert, f. nov. Planta usque ad 7.5 cm. alta, articulis regulariter cuneatis, rarum ovatis, inferioribus 7.5 mm. latis, 1.0 cm. longis, superioribus minoribus.

TYPUS: *H. H. Bartlett 15002*, ex Dalupiri Island, Babuyan Group, Insulis Philippinensibus, 31 X–5 XI, 1935, in Herb. Univ. Michiganensi.

This form reaches a height of 7.5 cm., with the segments nearly all typically cuneate, becoming smaller towards the tips of the branches. The shape of the cuneate segments is quite intermediate between the discoid segments of f. *typica* and the narrowly cuneate to digitate shape of most of the segments of f. *subdigitata*. The segments are generally not as broad as long.

Collections: *Bartlett 15002*, TYPE, *15003*, *15005*, *15010*, all from Dalupiri Island, Babuyan Group, 31 Oct.–5 Nov.; *A–41*, Lagoon of Big Santa Cruz Island, opposite Zamboanga, Jan.–Feb.; *A–90*, near Philippine Desiccated Coconut Factory, Zamboanga, Jan.–Feb.; *Balhani 66*, Atong-atong, near Malamaui, N. coast of Basilan Island, Jan.–Feb.; *214*, *Baliwasan* (Baliuasan), N. W. of Zamboanga, Jan.–Feb.; *386*, Manicaan (Manicahan), 15 miles N. E. of Zamboanga, Jan.–Feb.

HALIMEDA MACROLOBA Decaisne, 1842, p. 118; Harvey, 1863, Phycol. Austr. **5**: *pl. 267*; Barton, 1901, p. 24, *pl. 3, f. 33–38*; Okamura, 1915, **3**(10): *pl. 149, f. 1–8*.

Collections: *Bartlett 15415*, Basco, Batan Island, Batanes Province, July; *14956*, Currimao, Ilocos Norte Province, Luzon, Oct.; *Merrill, Species Blancoanae No. 993*, coral reefs, Puro, San Fernando, Union Province, Luzon, Oct. (as *Halimeda* sp.); *Yates, Bureau of Science 25829*, Basiad, Tayabas Province, Luzon, Dec.; *Villaflores 44*, Lubang, Mindoro Province, Sept.; *Bartlett 13932*, *13964*, *14059*, vicinity of Puerto Galera, Mindoro, May; *Velasquez 733*, *744*, *761*, *863*, *882*, *991*, *1016*, near Puerto Galera, Mindoro, March and April; *Bartlett 15574*, small island opposite Culion Harbor, Culion Island, Calamian Group, July; *Merrill 9151*, Taytay, Palawan, April; *Fénix, Bureau of Science no. 15815*, Zamboanga, Mindanao, Aug.; *Ebalo A–8*, Tumakid, Basilan Island, Jan.; *Balhani 305*, Bilang-bilang, Zamboanga Province, Jan.–Feb.; *719*, *751*, *773*, Basilan Island, Jan.–Feb.; *736*, Baluk-baluk Island, W. of Basilan Island, E. of Pilas Island, Jan.–Feb.; *J. B. Steere*, Balabac Island (no collection number or date.)

Halimeda orientalis Gilbert, sp. nov. Figure 1. Planta (in fluido) usque ad 6.0 cm. alta, multi-ramosa in parte inferiore; basi rhizoideo inconspicue;

[2] To the writer it now appears rather doubtful that *Halimeda cuneata* Hering is as widely distributed as formerly indicated. It has been reported from a number of places such as Japan, Liu-kiu Islands, China Sea, Formosa, Malay Archipelago, and New Guinea, as well as from Natal Bay in South Africa whence it was first described. The writer has not seen material from any locality other than South Africa which proved to be *H. cuneata* although several sets have been studied that were published and distributed as that species from regions other than South Africa, as, for instance, Yamada's Liu-kiu plant and Higashi's material from Hamajima, Shima. Instead the plants usually prove to be *Halimeda discoidea* Decaisne.

articulis circa 9 mm. latis, 6 mm. longis, minus quam 1.0 mm. crassis, interdum inconspicue nervatis; inferioribus crassis, ad basin subcuneatis vel subtruncatis, margine integerrimis aut conspicue lobatis, interdum conjunctis; superioribus complanatis, orbiculatis vel reniformibus, margine integerrimis aut crenulatis. Filamenta centralia haud cohaerentia, membrana solum ad apicem articulorum inerassata. Utriculi corticis non cohaerentes, pyriformes vel subclavati, 26–41 μ lati, 36–72 μ longi, modice calce incrustati.

TYPUS: *Liborio E. Ebalo A-20*, ex Tumakid, Basilan Island, Insulis Philippinis, January, 1941, in Herb. Univ. Michiganensi.

This new species of *Halimeda* reaches a height of 6.0 cm., but the usual height is about 5 cm. Branching near the base is abundant and in more than one plane so that a thick tuft of branches is formed (somewhat as in *H.*

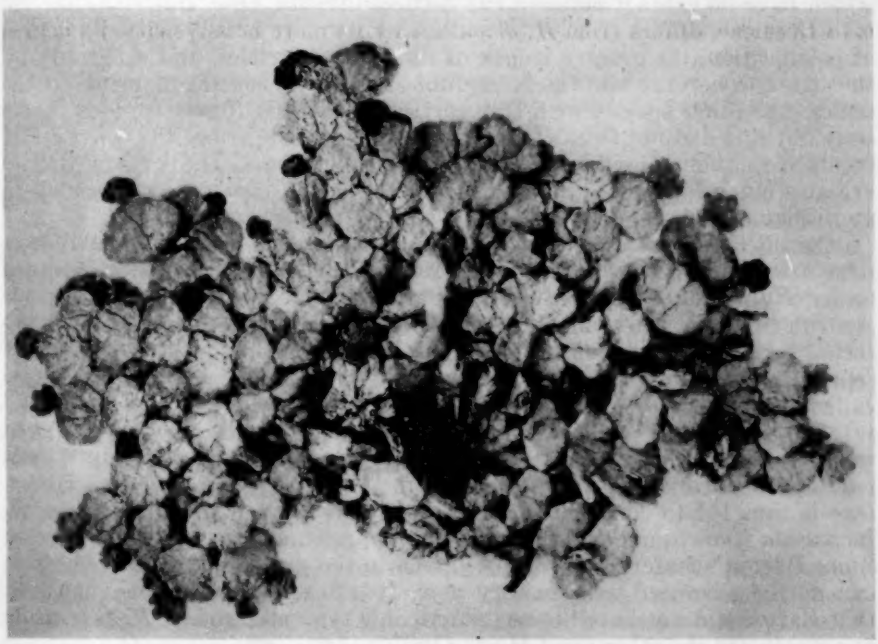

FIG. 1. *Halimeda orientalis* Gilbert, sp. nov. ×1.5.

Opuntia). Above the branches are fewer and more or less in one plane. The rhizoidal base is indistinct. Near the base of the plant the segments are irregularly cuneate or truncate, are thickened, and may be either entire or three-lobed. In some instances the basal segments are fused together and are many lobed. Above the segments are clearly flattened, discoid to somewhat reniform, with an entire or crenulate upper margin. Occasionally cuneate and truncate bases are found in the terminal segments. The normal segments reach a width of 9 mm. or less, which may be exceeded in the occasional fused segments at the base of the plant, and they are 6 mm. or less in height. In thickness the segments are less than 1 mm. Some of the segments are indistinctly ribbed. The central filaments at the apex of the segments have thickened walls but are entirely free. They are loose in the upper nodes, crowded

in the lower nodes, without pits, and easily separable upon teasing. The cortical utricles are pyriform to subclavate and are not coherent. Being free they are held together only by the deposition of lime and thus readily fall apart upon decalcification. The average maximum diameter of the cortical utricles is 37 μ, ranging from 26–41 μ. In length the cortical utricles are 36–72 μ. The subcortical utricles are equal to or less than the diameter of the of the peripheral utricles. Calcification is only moderate, and when dry the segments are whitish to greyish green, darker above.[3] Collection: *Ebalo A-20*, TYPE, Tumakid, Basilan Island, January.

This new *Halimeda* is characterized by the noncoherence of both cortical utricles and central filaments and by branching in more than one plane. Regarding coherence of utricles two other species of Halimeda are recognized which have no contact between the cortical utricles. One, *Halimeda macroloba* Decaisne, differs from *H. orientalis* by its more massive size, its degree of calcification, the greater length of its cortical utricles, and especially by the strong coherence and intercommunication of its central filaments at the nodes. The other species with free cortical utricles is *H. macrophysa* Askenasy but it is distinct from *H. orientalis* since in the former the central filaments are actually fused in twos and threes at the nodes. The cortical utricles are also much larger. Neither *H. macroloba* nor *H. macrophysa* branch in more than one plane.

Considering next the characteristic of free central filaments attention is drawn to the plants which Barton (1901, p. 27, *pl. 4, f. 42, 47*) included under *Halimedia incrassata* (Ellis & Solander) Lamonroux f. *ovata* (J. Agardh) Barton. These not only somewhat resemble the new species in external form but Barton noted that the central filaments at the apex of the segments are entirely free or connected by small and few pits. Barton also called attention to the occasional absence of pits in other forms of *H. incrassata* but spoke of free central filaments only in the plants which were placed under f. *ovata*. The similarity between the free central filaments in *H. orientalis* and Barton's figures of the same for *H. incrassata* f. *ovata* is striking. One is thus led to consider whether the plants Barton included under *H. incrassata* f. *ovata* might not actually be (in part, at least) the new species. Since Barton's material has not been seen in the present study this question can not be answered with finality now. It is interesting to note, however, that Barton did not have access to Agardh's type material of *H. incrassata* var. *ovata*. On the other hand Howe (1907, p. 503), who did make a detailed study of the type material of *H. incrassata* var. *ovata*, for comparison with *H. simulans*, made no mention of either free central filaments or noncoherence of cortical utricles. It seems most certain that if either central filaments or corticle utricles had been free it would have been noted by Howe for *H. simulans* has strongly coherent central filaments at the segment apices, as well as coherent utricles.

[3] In conjunction with the present study the writer was privileged to work on the green algae of a collection from the Netherlands East Indies which was made in 1938 by Dr. A. J. Kostermans with the cooperation of the Laboratorium voor Onderzoek der Zee, Batavia. In it is a plant collected at Seboekoe, Lampoeng Bay, Sumatra, which is unquestionably the same as the present proposed species. It is somewhat more robust, however, reaching a height of 9 cm., with the segments as large as 12 mm. in width and 8 mm. in height.

With reference to the manner of branching *Halimeda Opuntia* is the only other species in which the branching is in more than one plane but it can be readily separated from *H. orientalis* by its coherent utricles, its characteristic manner of incomplete fusion of central filaments at the apex of the segments, and by its distinctly ribbed segments.

Halimeda orientalis stands in the section of the genus in which the central filaments are not fused, probably closest to *H. macroloba* on the basis of noncoherence of cortical utricles and next to *H. tridens* (*H. incrasata*), especially those forms in which the pits between the cohering central filaments are few or wanting.

HALIMEDA OPUNTIA (L.) Lamouroux f. TYPICA Barton, 1901, p. 20, *pl. 2, f. 19*. The segments are distinctly ribbed, giving the upper margin a lobed appearance; the lower margins of the segments are about at right angles with the midribs, the joints not overlapping.

Collections: *Albatross Expedition 14; McGregor 47*, Calayan Island, Cagayan Province, (1903); *Bartlett 14619*, July, *15006*, Nov., Dalupiri Island, Babuyan Group; *Yates, Bureau of Science no. 25830 pp.*, Basiad, Province of Tayabas, Luzon, Dec.; *Villaflores 23*, Lubang Island, Mindoro Province, Sept.; *Bartlett 13933*, Puerto Galera, Mindoro, May; *Velasquez 761, 793, 823, 883, 1013, 1067*, all in April, vicinity of Puerto Galera, Mindoro; *Bartlett 16182*, Liloan Beach, E. coast of Cebu Island, Sept.; *Santos 649, 700*, vicinity of Puerto Princesa, Palawan, April; *Bartlett A–198*, Little Santa Cruz Island, opposite Zamboanga, Mindanao, Jan.–Feb.; *Ebalo A–13, A–21, A–32*, Basilan Island, Jan.–Feb.; *Balhani 67, 111, 123, 178, 235, 275, 290, 325, 352, 371, 387, 407, 408, 425, 440, 454, 483, 497, 508, 525, 526, 545, 566, 589, 603, 654, 682, 718, 737, 738, 752, 774, 818, 828, 829*, all from the vicinity of Zamboanga, Mindanao, and Basilan Island, Jan.–Feb.; *Bartlett 16121, 16122*, N. Ubian Island, Sulu Archipelago, Sept.

In the specimens above there is evident variation toward other forms which involves either the whole specimen or merely a part of it, often the latter. Portions of *Bartlett A-198* and *16122* come close to f. *triloba* while *Bartlett 16182* approaches f. *cordata*. Likewise *Balhani 526, 818*, and *829* approach f. *hederacea* with a segment here and there having the typical "ivy-leaf" shape of that form.

HALIMEDA OPUNTIA f. CORDATA (J. Agardh) Barton, 1901, p. 20, *pl. 2, f. 21; H. cordata* J. Agardh, 1886, p. 83. The segments are rounded above and at their bases cordate with the auriculate projections overlapping the segments below. Collection: *Merrill 9141*, Taytay, Palawan, April.

HALIMEDA OPUNTIA f. TRILOBA (Decaisne) Barton, 1901, p. 20, *pl. 2, f. 20; H. triloba* Decaisne, 1842, p. 102. In this form the segments are distinctly trilobed, especially in the lower portion of the plant, rather thick, and with evident ribs.

Collections: *Albatross Expedition no. 29; Bartlett 15883, 15589*, from small island opposite Culion Harbor, Culion Island, Calamian Group, July; *Velasquez 994*, Paniquian Island, vicinity of Puerto Galera, Mindoro, April; *Bartlett 16198*, Cebu Island, Sept.; *16146*, Little Santa Cruz Island, Basilan Strait, Zamboanga, Mindanao, Sept.; *Balhani 257*, Calarian (Kaladian) near Army Post, Zamboanga, Jan.–Feb.; *613, 792*, Basilan Island, Jan.–Feb.; *Bartlett 16035*, Siasi Island, Sulu Archipelago, Sept.

There is considerable variation among the specimens representing this form. *Bartlett 15589*, for instance, has the upper parts approaching f. *typica*

while the lower parts are unmistakably like f. *triloba*. Specimens of *Bartlett 16035* are in good fruiting condition and it is interesting to note that the tufts of sporangia originate from the tips of the lobes instead of along the entire upper margin.

HALIMEDA OPUNTIA f. RENCHII (Hauck) Barton, 1901, p. 21, *pl. 2, f. 22, 22a; H. Renchii* Hauck, 1886, p. 167. In this form the segments are comparatively small, round, cuneate or ovate, and with indistinct ribs; the branches more or less radiate from a common center. Collections: *Bartlett 15007, 15008*, Dalupiri Island, Babuyan Group, Nov. Approaching in part f. *intermedia* Yamada, *Bartlett 15008* appears to represent a transition between the two forms.

HALIMEDA OPUNTIA f. INTERMEDIA Yamada, 1934, p. 81, *f. 50, 51*. The segments are round or ovate, or sometimes with slightly cordate bases, and in appearance are much like the segments of f. *Renschii* but larger, varying in size and reaching 8 mm. in width and 6 mm. in height. Collection: *Santos 118*, Wawa, Nasugbu, Batangas Province, July. This specimen is fruiting and the tufts of sporangia are quite evenly distributed along the entire upper margin of the segments.

HALIMEDA OPUNTIA f. HEDERACEA Barton, 1901, p. 21, *pl. 3, f. 23*. The segments are usually large, trilobed, having the appearance of an ivy leaf, and with distinct ribs.

Collections: *Yates, Bureau of Science 25830 pp.*, Basiad Tayabas Province, Luzon, Dec.; *Ebalo A–33*, Punta Mangal, Basilan Island, Jan.; *Balhani 256*, Calarian (Kaladian) near Army Post, Zamboanga, Jan.–Feb.; *614*, Liksapi, near Bagbagon, Basilan Island, Jan.–Feb.; *Albatross Expedition 14a*.

The segments are nearly always larger than in other forms of *Halimeda Opuntia*, reaching a width of 18 mm. and height of 13 mm. or less. The surface of the segments is often shiny. Seldom do all of the segments exhibit the ivy-leaf shape as one might suppose from Barton's descriptions and figure, but in *Ebalo A-33* most of the segments are of the typical shape. In *Balhani 256* many of the segments have a cordate base, thus approaching *H. Opuntia* f. *cordata*.

HALIMEDA MONILE (Ellis & Solander) Lamouroux, 1812, p. 186; *Corallina Monile* Ellis & Solander, 1786, p. 110, *pl. 20, f. c; H. incrassata* f. *monlis* Barton, 1901, p. 27, *pl. 4, f. 40*. Collection: *Bartlett 15578*, small island opposite Culion Harbor, Culion Island, Calamian Group, July.

HALIMEDA TRIDENS (Ellis & Solander) Lamouroux f. TYPICA (Barton) Collins, 1909, p. 318; *H. incrassata* (Ellis & Solander) Lamouroux f. *typica* Barton, 1901, p. 27, *pl. 4, f. 39*. In this form the lower segments are cylindrical or somewhat compressed, sometimes fused to form a fan-shaped base; the upper segments are distinctly compressed, entire or crenulate, or at times trilobed.

Collections: *Yates, Bureau of Science no. 25831*, Basiad, Province of Tayabas, Luzon, Dec.; *Ebalo A–12*, Tumakid, Basilan Island, Jan.; *Barlett A–88*, near Philippine Desiccated Coconut Factory, Zamboanga, Jan.–Feb.; *Balhani 158*, Lanhil (Little Sibago)

Island (at E. entrance to Strait of Basilan), Jan.–Feb.; *427*, Labuan, 20 miles N. W. of Zamboanga, Jan.–Feb.; *524*, *604*, Basilan Island, Jan.–Feb.; *Bartlett 16130* and *16132*, North Ubian Island, Sulu Archipelago, Sept.; *16033* and *16037*, S. of Siasi, Siasi Island, Sulu Archipelago, Sept.

HALIMEDA TRIDENS f. **Lamourouxii** (J. Agardh) Gilbert, comb. nov. *Halimedia incrassata* var. *Lamourouxii* J. Agardh, 1886, p. 86. The lower segments are compressed and broadly cuneate, sometimes lobed; the upper segments are thin, cuneate to discoid, or reniform, with a crenulate or lobed margin; the segments are large and heavily calcified. Collections: *Bartlett 15584*, small island opposite Culion Harbor, Culion Island, Calamian Group, July; *A-196*, Little Santa Cruz Island, opposite Zamboanga, Jan.–Feb.

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DEPARTMENT OF BIOLOGY, ALBION COLLEGE
ALBION, MICHIGAN

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ON THE GENUS MITRASTEMON

EIZI MATUDA

INTRODUCTION

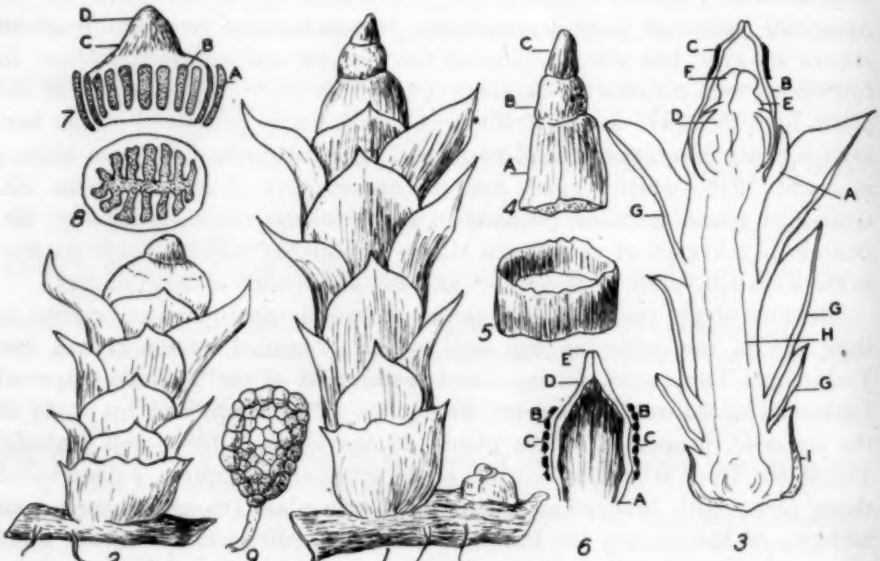
In March, 1934, while on an expedition to Mt. Ovando, which is in the municipality of Escuintla, Soconusco district, state of Chiapas, southern Mexico, and while in the so-called *Quercus* vegetational zone at an altitude of 1700 meters, I unexpectedly found a parasitic plant which I instantly recognized as a species of *Mitrastemon*. The existence of this genus on the American continent is most surprising. For a moment it was difficult to believe my eyes, but since I collected this curious and interesting plant, in full bloom, with my own hands, there could be no doubt. My collection of the plant, both in flower and in fruit, was subsequently preserved in the herbarium of my plantation "La Esperanza," near Escuintla. Two years later—in April, 1936—when I again had the opportunity of botanizing on Mt. Ovando, I found the same parasite in abundance at the same locality. Mt. Ovando is a branch of the Sierra Madre of Chiapas which pushes its way to the so-called valley of Soconusco and has an altitude of 2300 meters.

Because of the fact that at that time I lacked any literature relative to these plants, my collection was sent to and examined by my friend, Dr. Yoshimatsu Yamamoto, distinguished taxonomist of the Taihoku Imperial University of Taiwan, Japan. Dr. Yamamoto, after completing his study of the material, proposed for the plant (1) the name *Mitrastemon Matudai* Yamamoto. Upon receipt of reprints of the original description, I distributed these, along with herbarium specimens of the plant, to all the principal herbaria of Mexico and the United States, but professional botanists there apparently gave the discovery very little attention.

In Europe, however, some excitement was caused by this discovery. Dr. Ludwig Diels, late director of the *Botanisches Museum und Garten* at Berlin, wrote to me asking for certain morphological details and for some specimens of the parasite. For the scientific world this was not only a new species, but constituted the record of a new genus and family for the continental American flora. Yamamoto's original description was drawn from a dry herbarium specimen, and should be corrected as follows from observations made on fresh material (figs. 1–9).

Planta parasitica ad radices horizontales *Querci boqueronae*, in vivo lactea nitidaque, in statu exsiccato fusco-nigricans nitidaque, 4–12 cm. longa, cum squamis imbricatis 3–3.5 cm. diam. Receptaculum basale cupuliforme crassum, ca. 1.5 cm. longum, ca. 2.5 cm. diam., plus minusve compressum furvum non nitidum (in vivo), nigro-fuscens non nitidum (in statu exsic-

cato) irregulariter tuberculatum, ad oram irregulariter lobatum, lobis saepe 4, margine rotundatis saepe 1–2-lobulatis. Caulis cylindricus, simplex, 1 cm. diam., erectus, 3–8 cm. longus, squamatus. Squamae imbricatim oppositae, vulgo 7-seriatim dispositae, glabrae nitidaeque in vivo lacteae ad apicem minute ferruginoso-nigricantes, in statu exsiccato ad faciem badiae vel fulvo-rubescentes, inaequilongae; squamae inferiores minores, apicem versus gradatim majores; squamae basales primariae 2 inter se oppositae late ovatae vel rotundatae 1.3 cm. longae, 1.5 cm. latae, ad apicem obtusissimae vel rotundatae intus concavae extus convexae et leviter longitudinaliter rugosae; squamae secundariae 2 inter se suboppositae et cum primariae alternae rotundatae 1.8 cm. longae, 2 cm. latae, ad apicem obtusissimae intus valde concavae, extus convexae; squamae mediae 2 inter se oppositae deltoideae vel late triangulares 2.8 cm. longae, ca. 2.5 cm. latae, ad apicem obtusae, intus



FIGS. 1–9. *Mitrastemon Matudai* Yam. Drawn from fresh material. Figs. 1–5 reduced to 0.9 natural size. FIG. 1. Plant in bloom, with mitriform cap of stamens. FIG. 2. Dwarfed plant, in fruit. FIG. 3. Longitudinal section of whole plant. A, perianth; B, mitriform cap of stamens; C, anther; D, ovary; E, style; F, stigma; G, scale; H, stalk; I, volva. FIG. 4. Stamen. A, connate filament; B, anther; C, point of anther belt. FIG. 5. Perianth. FIG. 6. Longitudinal section of anther belt. A, anther belt; B, pollen sac; C, mucous; D, point of the belt; E, slit. FIG. 7. Mature ovary in longitudinal section. A, perianth; B, ovules; C, conical point. FIG. 8. The same in cross section. FIG. 9. Ovule.

valde concavae extus valde convexae; squamae superiores deltoideae 2 inter se oppositae 2 cm. longae, 2.2 cm. latae, ad apicem obtusae extus convexae, intus concavae et superne valde involutae falciformiter inflexae. Perianthium membranaceum, gamophyllum, breviter cylindricum vel circuliforme, 6 cm. longum, 1.5–1.7 cm. diam., extus longitudinaliter paralleliterque rugosum, in statu exsiccato badium, sed in vivo lacteum, ad oram irregulariter undu-

latum. Androecium hypogynum, calyptriforme, ad apicem obtusum; tubo filamentorum connatorum 2.8 cm. longo, 1.4 cm. diam. glaberrimo lacteo in vivo, extus longitudinaliter paralleliterque striato in statu exsiccato; tubo antherarum 8 mm. longo, 12 mm. in diam.; tubus androecii ultra antheras productus pyramidalis vel conicus, 3 mm. longus, ad basim 5 mm. diam., longitudinaliter 3-seriatim striatus, seriebus 4 linearibus in statu exsiccato. Fructus solitarius terminalis, erectus sessilis baccatus teres, sed ad faciem longitudinaliter plus minusve sulcato-striatus, cupuliformis vel breve cylindricus et valde compressus, 1 cm. longus, 1.5 cm. diam., unilocularis; placentis 15 crassiusculis lamellatis, stylo brevissimo 2 mm. longo, stigmate conico 7 mm. longo et 7 mm. diam. Semina minima, plurima, obovata, stipitata, ad faciem reticulata.

HISTORY OF THE GENUS

The genus *Mitrastemon* was established in 1909 by Dr. Tomitaro Makino (2), based on a single parasitic species, the type specimen being flowering but of very peculiar character, collected in Koti prefecture, Sikoku, on the southern island of Nippon proper, by Prof. H. Yamamoto of the Normal College of that prefecture. However, this parasite had been widely known to the natives of Kagosima prefecture on Kyusyu—another southern island of Nippon proper—under the name of "Hanasii no Titi," and had actually been recorded in literature by A. Tasiro more than thirty years before Makino's description appeared. Dr. Makino, after further study of more and perfect material of the plant, published another account of it in 1911 and made the proposal entitled "Serie Mitrastemonales, nov.; Fam. Mitrastemonaceae, nov." (3). This marked a new epoch in the history of plant taxonomy in Japan.

In the same year at Mt. Muto in Taiwan (Formosa), then a southern territory of Japan, specimens of another parasite were collected by Eng. T. Kawakami and S. Sasaki. In 1912 Dr. Bunzo Hayata, the well-known systematic botanist of the Tokyo Imperial University, named this new species *Mitrastemon Kawa-Sasakii* Hayata (4). In 1913 Hayata published his opinion relative to the systematic position of *Mitrastemon*, assigning it to the family Rafflesiaceae in his *Icones plantarum formosanarum* (5). This disposition was adopted by Engler in *Die natürlichen Pflanzenfamilien* (6), and also in Engler & Gilg's *Syllabus der Pflanzenfamilien,"* edition 8 (7).

Meanwhile, in Taiwan another new parasitic plant was discovered which was identified by Dr. Y. Yamamoto as a third species, *Mitrastemon Kanehirai* Yam. (8). While occupied in botanical research in southern Taiwan, the writer also collected *M. Kawa-Sasakii* on Mt. Minami-daibu in 1919. In 1929 Dr. Jechens collected a parasite at Brentagi in northern Sumatra, Netherlands East Indies, and this was determined by Dr. Hayata as *M. Kawa-Sasakii* (9).

OBSERVATIONS

The general appearance of these parasites will be understood from the description given above of *M. Matudai*. All the species have approximately the same aspect. The plants are beautiful when alive, resembling wax art work with their shiny lacteous surface. They grow on the horizontal roots of members of the family *Fagaceae*. I have observed that the height of the plant seems to depend on the depth of the host root. Usually there are four upper scale-leaves on the surface of the ground. The root may be from 4 to 10 cm. underground, never deeper. It is a notable fact that in any one region the parasite utilizes as host the roots of only a single species. *M. Matudai* grows only on the roots of *Quercus boqueronae*, on Mt. Ovando in southern Mexico, as far as I am aware. *M. Yamamotoi* Mak. grows on *Shiia Sieboldi* Mak. in Koti, Sikoku, and on *S. cuspidata* Mak. in Kagosima, Kyusyu. *M. Kawa-Sasakii* Hay. grows on *Quercus glauca* Thunb. on Mt. Muto, Taiwan, on *Lithocarpus Kawakamii* Hay. on Mt. Reito, Taiwan, on *Symaedrys brevicaudata* Koidz. on Mt. Roppei, Taiwan, and on *Quercus spicata* Sm. in Sumatra. *M. Kanehirai* Yam. grows on *Castanopsis Kawakamii* Hay. in Rengeti and on *C. taiwaniana* Hay. in another locality on Taiwan.

Although this parasitic genus has a rather wide distribution from the southern islands of Japan proper down through Okinawa, Taiwan, and as far south as Sumatra, below the equator, the climatography of each locality has a definite similarity. For instance, at the northern limit of Koti prefecture we have:

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Average
Temperature	5.4	6.1	9.5	14.7	18.1	21.6	25.2	26.1	23.1	*17.8*	*12.8*	7.2	15.6 C.
Rainfall	66	103	87	284	282	345	326	307	420	*216*	*114*	78	227 mm.

In Koti prefecture the parasite has been collected in October and November, as is indicated by the italic in the table above.

In Kagosima prefecture, as an example of the middle zone of distribution, the following climatic conditions are noted:

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Average
Temperature	10	10	14	14	18	22	28	28	26	22	*18*	*12*	20 C.
Rainfall	100	100	150	150	200	400	250	150	250	200	*100*	*50*	200 mm.

Here, as indicated by the italic, it has been collected in November and December, during the dry season, with the temperature ranging from 12° to 18° C.

On Mt. Muto, in southern Taiwan, in the *Fagaceae* zone, where the plant is found at an altitude of approximately 1400 meters, we observe the following conditions:

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Average
Temperature	*11.4*	*11.4*	11.4	13.4	15.4	19.4	19.4	19.4	19.4	17.4	13.4	11.4	15.4 C.
Rainfall	*35*	*75*	75	75	225	450	550	800	450	175	125	35	275 mm.

Here the italic indicates that the plant grows in January and February, during the dry season, with the temperature at about 11.4° C.

In Sumatra, according to information given by Jochems, at Brastegi, at an altitude of 1500 meters, we have the following conditions:

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Average
Temperature	16.0	16.9	17.7	17.4	18.1	17.5	17.7	18.1	17.6	17.3	17.5	17.5	17.4 C.
Rainfall	206	98	159	219	115	59	109	151	132	175	221	252	157.8 mm.

In Brastegi, where a temperature of 16° to 18° C obtains all through the year, *M. Kawa-Sasakii* grows all the year round.

Lastly, in Mexico, on Mt. Ovando the parasite grows only from February to April, during the dry season, when the temperature is from 14° to 16° C.

The figures quoted above, therefore, show that *Mitrastemon* grows only in temperatures ranging between 10° and 20° C and principally during the dry season when the activities of the host tree are at a minimum. When the plants are in bloom honey-like fluids with a special odor are secreted at the basal portion of the peduncles. These fluids attract various insects and a large number of little birds. In Kagosima the local name of the parasite is "Hanasii-no-Titi," which signifies "milk of meziro" (the "meziro" is a favorite little bird, *Zosterops japonica* T. & Z.). From Taiwan it is reported that one of the insects attracted is *Vespa magnifica* var. *nobilis* Sonan, and in Sumatra a species of *Drosophila*. In Mexico the writer has secured two species of insects from the plant, but they have not yet been identified. Pollination is, naturally, accomplished by these birds and insects.

KEY TO THE SPECIES

I have made mention of the three species of *Mitrastemon* which we know from Japan and Sumatra, namely, *M. Yamamotoi* Mak., *M. Kawa-Sasakii* Hay., and *M. Kanehirai* Yam. Now, however, according to Makino, the last two species are recognized as merely varieties of the first (10).

A key for the identification of these species and varieties follows.

Plant height 3–6 cm.; scales in 6 pairs, opposite, imbricate. (In Japan proper and Okinawa.) *M. Yamamotoi* Mak.

Plant height 15 cm.; scales oblong, in 6 pairs. (In Taiwan and Sumatra.) *M. Yamamotoi* var. *Kawa-Sasakii* (Hay.) Mak.

Plant height 6–8 cm.; scales in 12 pairs; 4-angled, obconic in form. (In Taiwan.) *M. Yamamotoi* var. *Kanehirai* (Yam.) Mak.

Plant height 4–12 cm.; scales broad, triangular, in 7 pairs; stigma conic; fruits appressed, cylindric. (In southern Mexico.) *M. Matudai* Yam.

SYSTEMATIC POSITION

The genus *Mitrastemon* is a very peculiar group, widely different from all other known flowering parasites. It is possible to find some affinities for it in each of the following five families: *Nepenthaceae* of Malaya, *Rafflesiaceae* of Indonesia, Africa, and tropical America, *Hydnoraceae* of Africa and tropical America, *Balanophoraceae,* and *Aristolochiaceae.* Affinity with the *Nepenthaceae* appears in (1) the superior ovary, and (2) the single perianth, but the structure of the flower and the fruit differs widely.

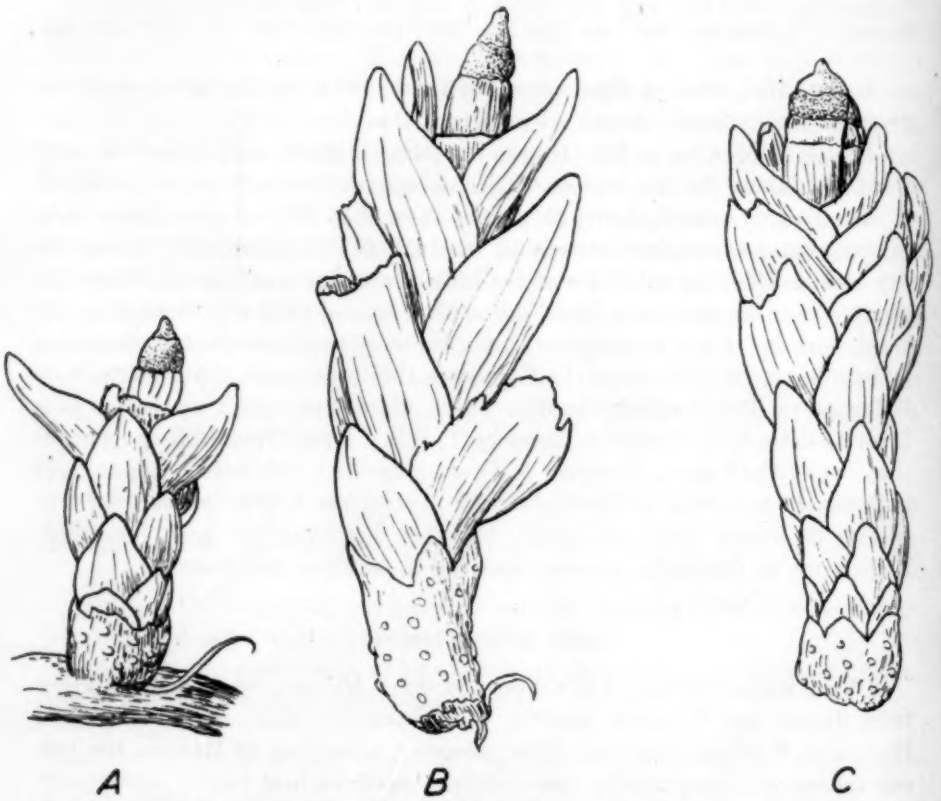


FIG. 10. A, *Mitrastemon Yamamotoi* Mak.; B, *Mitrastemon Yamamotoi* var. *Kawa-Sasakii* (Hay.) Mak.; C, *Mitrastemon Yamamotoi* var. *Kanehirai* (Hay.) Mak. All natural size.

There are many similar morphological and anatomic characters which point to the *Rafflesiaceae,* as has been pointed out and discussed by Hayata—for instance, (1) it is a parasite, (2) is hermaphrodite, (3) is leafless but bears scales, and (4) has a one-celled ovary with parietal placentae. Differences are seen in (1) the superior perianth, (2) anthers growing on single

or several lines, (3) the inferior ovary, and (4) the disk-like torus on which the anthers grow, etc.

As to the *Hydnoraceae* the points of likeness are (1) the parasitic nature of the plants, (2) the single hermaphrodite flowers, and (3) the perianth-tube. But they differ in (1) the 3–4-lobed perianth, (2) the anthers placed in 1 or 2 series attached to the perianth-tube, and (3) the epigynous, sessile filaments, etc.

With the *Balanophoraceae* there is close affinity in (1) the parasitic nature, (2) the single, unbranched stems with scales, (3) the basal volva, and (4) the hypogynous androecium. But there is dissimilarity in (1) the multiflowered or saraceous peduncle, (2) the mostly diclinous flowers, (3) the 3–4-lobed perianth, (4) the 1–8-celled anther, and many other differences in the principal structure of the flower.

Finally, it resembles the *Aristolochiaceae* in its (1) coherent perianth, (2) baccate fruits, (3) anatropous ovules; but the latter family is easily distinguished by its (1) superior perianth, (2) epigynous flower, and (3) leafy and not parasitic nature.

Above all, our genus is characterized by its (1) mitriform, united, connate stamens, (2) hypogynous flowers, and (3) anatropous ovules, in which it is distinct from all the other families. After considering the extent of the differences from the above five families, we are forced to the conclusion that *Mitrastemon* forms an independent family, as suggested by Makino and recently approved by Honda and Sakisaka in their *Plant Taxonomy of Nippon* (12, 14). The *Mitrastemonaceae* should be placed between the *Rafflesiaceae* and the *Hydnoraceae*.

DISTRIBUTION

Since the first discovery of *Mitrastemon* unusual attention has been given to this group of parasites, and specimens have been collected in many localities where it was hitherto not known to exist. The genus is now reported from the Tokusima prefecture, northeast of Koti, where it was first discovered, on the same island of Sikoku, and this is its northern limit. In the Koti prefecture it has been collected extensively in many *Shiia* zones; also, it is newly reported from the Miyazaki prefecture on the island of Kyusyu, northeast of the Kagosima locality previously mentioned. In the Kagosima prefecture it is now also widely known in the *Shiia* zone, and it is also reported on the small islands of Amami-osima and Yakusima of the same Kagosima prefecture. The range of distribution extends south to Okinawa, a prefecture of the Ryukyu Archipelago. In all these localities only the one species, *M. Yamamotoi,* is known.

In Taiwan it is widely known from the north to the south in the temperate zone of *Fagaceae,* but only in the varieties *Kawa-Sasakii* and *Kanehirai.* The

first of these varieties ranges as far south as Sumatra. At Rengeti, in the center of Taiwan, both of the varieties have been found practically intermingled, but always on hosts of separate species.

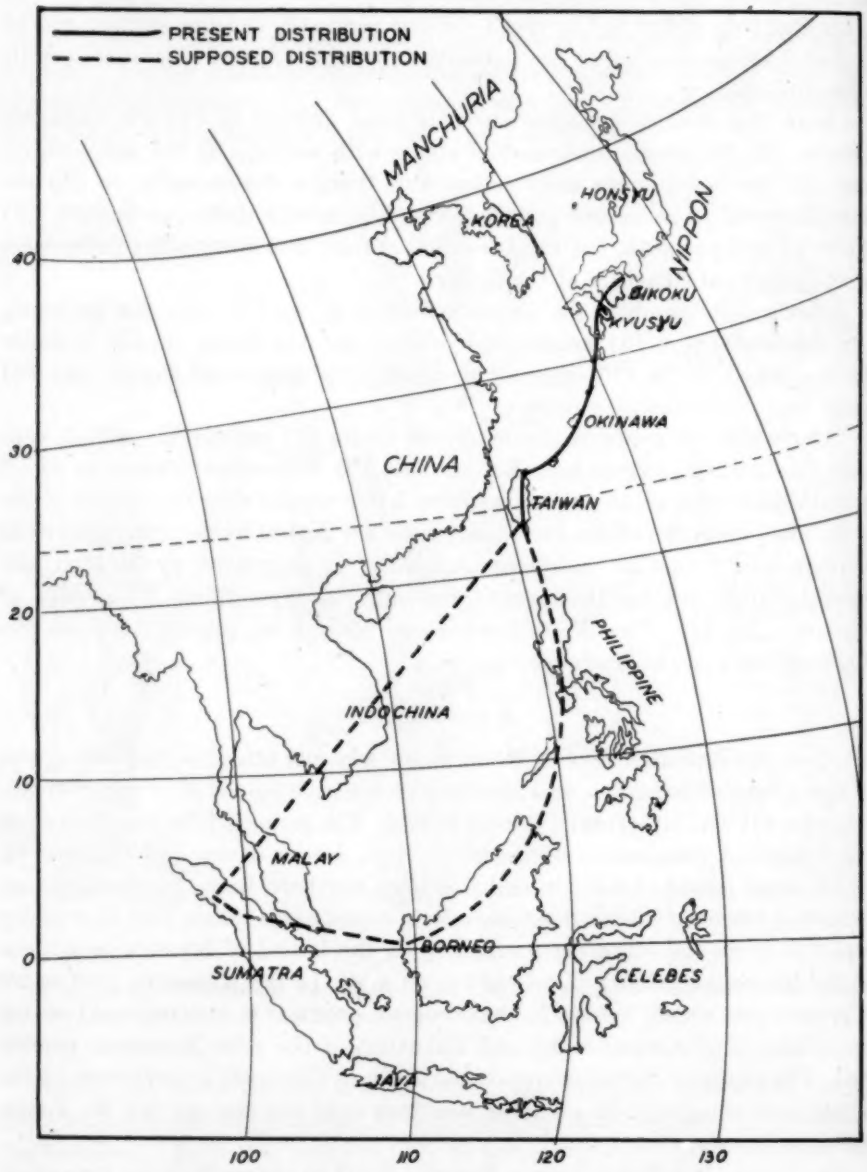


FIG. 11. Distribution of *Mitrastemon* in eastern Asia.

In the near future it may possibly be found in Malaya, Borneo, and the Philippines, in which case the geographic distribution of *Mitrastemon* would stretch from Sumatra to southern Japan, forming an arc in eastern Asia (fig. 11).

Very recently it has been reported that *Mitrastemon Matudai* has been found by Paul C. Standley at Altaverapaz, Guatemala (11–14).

The new appearance of *Mitrastemon* in southern Mexico and in Guatemala, beyond the vast Pacific Ocean, presents a great puzzle to geobotanists. It will prove exceedingly difficult to harmonize this with the generally accepted tenets of the Darwinian theory of evolution.

MATUDA HERBARIUM
ESCUINTLA, CHIAPAS, MEXICO

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NOTES ON THE COMPOSITAE OF THE NORTHEASTERN UNITED STATES—V. ASTEREAE

ARTHUR CRONQUIST

This series of papers is being presented in order to validate certain nomenclatural changes necessitated in preparing the treatment of the *Compositae* for Dr. Gleason's new illustrated flora of the northeastern states, and to allow for more ample discussion of some of those changes than is possible within the confines of a flora. Several previous numbers in the series have appeared in Rhodora. The present paper deals principally with *Aster,* but also includes the other *Astereae* except *Solidago,* on which a separate paper has been prepared for Rhodora.

Several years ago, when I was revising the western representatives of the *Aster foliaceus* complex, I noticed that the eastern American plants which had been referred to *A. foliaceus* Lindl. could generally be recognized at a glance, purely by their habit. These specimens, furthermore, were in some respects (such as the commonly toothed leaves) nearer to *A. douglasii* Lindl. than to *A. foliaceus.*

Upon re-examination of these eastern plants, I am convinced that they should be distinguished specifically from their western relatives. The habit difference previously noted is largely a matter of the conspicuously crowded cauline leaves of the more common eastern phase of the species. Another significant character, although it is not always well shown in herbarium specimens, is that *A. foliaceus* tends to have well developed basal leaves (often on separate short shoots) which are larger and more petiolate than those above, while eastern plants tend to have the lower leaves similar to or smaller than those above, without any basal cluster. The lower leaves may sometimes be deciduous before flowering in *A. foliaceus,* but are uniformly so in eastern plants.

Another factor to be considered in reaching a decision on the status of the eastern plants is that their greatest similarity is not to *A. foliaceus* proper, but to apparent hybrids between that species and *A. douglasii.* Inclusion of the eastern plants in either of these species would seemingly necessitate the reduction of the other, although each of them is already broadly defined and highly variable.

Three specific names should be considered before a new name is proposed for the eastern plants under discussion. *Aster johannensis* Fern., from Lake St. John, resembles *A. novi-belgii* L. in habit, but has narrower, more appressed phyllaries, much as in *A. junciformis* Rydb. An isotype at New York

seems reasonably typical of *A. novi-belgii*. Two collections from James Bay (*Dutilly 13347* and *13479*), where *A. novi-belgii* is otherwise unknown, closely resemble the type of *A. johannensis*, suggesting that it may prove to be more than merely an extreme form of *A. novi-belgii*. In any case, these plants are not the same as the eastern species that has been referred to *A. foliaceus*.

Aster anticostensis Fern. appears to be either an unusual form of *A. novi-belgii* or possibly a hybrid involving that species.

Aster gaspensis Vict. is apparently a good species, with relatively narrow, mostly entire, scarcely or not at all auriculate leaves, and with more elongate inflorescence and less leafy involucre than the eastern plants of "*A. foliaceus*." A number of collections from the vicinity of Lake Mistassini which have been referred to *A. foliaceus* seem more properly to belong to *A. gaspensis*.

Since there seems to be no available specific name for the eastern relatives of *A. foliaceus* under discussion, I am elevating one of the several proposed varieties to specific rank.

Aster crenifolius (Fern.) Cronquist, comb. nov. *A. foliaceus* var. *crenifolius* Fern. Rhodora **17**: 15. 1915.

Most of the specimens of *A. crenifolius* have conspicuously crowded leaves, with the middle and upper internodes mostly 5–30 (or 35) mm. long, but a number of plants, chiefly from more protected habitats such as alluvial stream-bottoms, have more distant leaves, with the middle and upper internodes mostly 3–6 cm. long. These latter specimens also differ in several scarcely tangible ways, giving the impression of being much laxer than the more typical plants. Although the ranges of the two are nearly or quite coextensive, it seems desirable to distinguish them varietally.

ASTER CRENIFOLIUS (Fern.) Cronquist var. **crenifolius** (Fern.) Cronquist, comb. nov. *A. foliaceus* var. *crenifolius* Fern. Rhodora **17**: 15. 1915. *A. foliaceus* var. *subpetiolatus* Fern. loc. cit., a robust form.

ASTER CRENIFOLIUS (Fern.) Cronquist var. **arcuans** (Fern.) Cronquist, comb. nov. *A. foliaceus* var. *arcuans* Fern. Rhodora **17**: 14. 1915. The laxer, less leafy plants referred to above.

Aster foliaceus var. *sublinearis* Griscom & Eaton is in my opinion merely an extreme form of *A. novi-belgii*, with more than usually leafy involucre. *A. foliaceus* var. *subgeminatus* Fern., still known only from the type collection in Newfoundland, is a puzzling plant which I do not feel able to place at present. Were *Aster ciliolatus* Lindl. known to occur in Newfoundland, I would be inclined to consider *A. foliaceus* var. *subgeminatus* a hybrid between that and *A. crenifolius*. Its status, in any case, has no apparent bearing on the distinctness of *A. crenifolius* from *A. foliaceus*.

It may also be pointed out that most of the material from Nova Scotia

referred to *A. foliaceus* by Shinners (Rhodora **45**: 344–351. 1943) is in my opinion *A. novi-belgii*, as is also *A. rolandii* Shinners.

It has been customary, in recent years, to separate *Aster falcatus* Lindl. from *A. commutatus* (T. & G.) A. Gray by its thinner, less squarrose, more acute involucral bracts, sparser pubescence, and more northern distribution. The morphologic characters are intangible and inconstant, and are scarcely to be made out at all without comparison of an extensive suite of specimens. The supposed difference in range is largely illusory. Specimens differing in the technical features noted look very much alike in other respects. Furthermore, there is no suggestion of discontinuity, or even modal distribution, in these supposedly distinctive features. I find it necessary, then, to combine the two species under the earlier name, *A. falcatus* Lindl.

In *Aster falcatus*, as in the closely related *A. ericoides* L., the majority of the specimens may be placed in two categories according to the orientation of the cauline pubescence, with only a relatively few intermediates. In spite of the fact that their ranges are essentially co-extensive, it therefore seems desirable to give these pubescence-types varietal recognition.

ASTER FALCATUS Lindl. var. **falcatus** Cronquist, var. nov. *A. falcatus* Lindl. in DC. Prodr. **5**: 241. 1836, sensu stricto. Hairs of the stem mostly appressed or closely ascending.

ASTER FALCATUS Lindl. var. **crassulus** (Rydb.) Cronquist, comb. nov. *A. crassulus* Rydb. Bull. Torrey Club **28**: 504. 1901. Hairs of the stem spreading.

As has been pointed out by Mrs. Nelson (Rhodora **35**: 323–325. 1933), cordilleran plants of "*A. ericoides*" have the stems clustered from a short rhizome or branched caudex. Mrs. Nelson was apparently unaware, however, that typical *A. ericoides* L., as it occurs in the eastern United States, regularly has the stems arising from well developed creeping rhizomes. It seems not unlikely that the cordilleran plants which have been referred to *A. ericoides* should properly be treated as a distinct species, to be distinguished by their cespitose habit and some less tangible or less constant features recorded by Mrs. Nelson, but I hesitate to do so at this time, for occasional cordilleran plants of otherwise apparently not unusual *A. falcatus* are also cespitose instead of creeping-rhizomatous. Until the significance of the cespitose versus creeping-rhizomatous habit in this group can be studied in greater detail, and especially in view of the fact that it is doubtful that there is an available specific name properly applicable to the cordilleran phase of "*A. ericoides*," I think it is better not to propose any formal taxonomic segregation.

In comparing specimens of *Aster paludosus* Ait., preparatory to drawing up a description, I noticed an extremely wide variation in the shape of the inflorescence. Some specimens showed a narrow, elongate, racemiform or

spiciform inflorescence, while others had the heads more loosely arranged in a broader, corymbiform inflorescence. These latter specimens, furthermore, had the inflorescence more obviously hairy than the others. Sorting the specimens on these characters revealed that those with the corymbiform inflorescence occur from North Carolina to Florida and Alabama, while the others range from Missouri and Kansas to Texas and Alabama. In Alabama, where the ranges meet (as, for example, in Cullman County), there are doubtful specimens; otherwise the distinction is seldom difficult. A good case might be made out for distinguishing the two phases as separate species, but they are obviously very closely related, and I think the taxonomic needs are in this case best met by use of the subspecific category.

In his treatment of the group for Small's flora of the southeastern United States, Alexander restricted the name *A. paludosus* to the eastern, more hairy plant, and divided the remainder of the group into four new species. These new species were distinguished from each other chiefly by the presence or absence of creeping rhizomes and the degree of imbrication of the involucral bracts. Both of these characters are frequently valuable in the genus, but in this case they seem to be independently variable and without taxonomic significance. Since the cultivated plants on which the original *Aster paludosus* of Aiton was based were stated to have come from Carolina, Alexander's selection of the typical element of the species may well be adhered to.

ASTER PALUDOSUS Ait. subsp. **paludosus** Cronquist, subsp. nov. *A. paludosus* Ait. Hort. Kew. **3**: 201. 1789, sensu stricto.

The more western, less hairy plants, with narrower and more elongate inflorescence may be known as *Aster paludosus* Ait. subsp. **hemisphaericus** (Alexander) Cronquist, comb. nov. (*A. hemisphaericus* Alexander in Small, Fl. S.E. U.S. 1391. 1933. *A. pedionomus* and *A. gattingeri* Alexander, loc. cit. *A. verutifolius* Alexander, ibid., p. 1392).

Dr. L. H. Shinners, among others, has pointed out that the name *Aster paniculatus* Lam. (1783) is antedated by *Aster paniculatus* Mill. (1768) and thus is illegitimate. The next available name which applies with reasonable certainty to Lamarck's species, so far as I am aware, is *A. simplex* Willd. Enum. Hort. Berol. 887. 1809. This is the relatively broad-leaved phase which Dr. Wiegand treated as *A. paniculatus* var. *simplex* (Willd.) Burgess. It becomes necessary, then, to find a varietal name for the narrow-leaved, chiefly northeastern phase of the species, which Wiegand treated as *A. paniculatus* proper. This is provided in *A. simplex* var. **ramosissimus** (T. & G.) Cronquist, comb. nov., based on *A. tenuifolius* β *ramosissimus* T. & G. Fl. N. Am. **2**: 132. 1841.

The small-headed midwestern plants which Dr. Wiegand segregated from *A. paniculatus* as *A. interior* Wieg. do form a definable entity, but pass readily into the larger-headed forms, and differ in no other apparent charac-

ter. I think it proper, then, to reduce them to varietal status. Since, as Dr. Wiegand showed, the type of *A. carneus* γ *ambiguus* T. & G. may be of hybrid origin rather than representing pure *A. interior*, it seems best to retain Wiegand's epithet in making the new combination.

ASTER SIMPLEX Willd. var. **interior** (Wieg.) Cronquist, comb. nov. *A. interior* Wieg. Rhodora **35**: 35. 1933.

The nomenclaturally typical variety of *A. simplex* may be known as *Aster simplex* Willd. var. **simplex** Cronquist, var. nov., based on *A. simplex* Willd. Enum. Hort. Berol. 887 (1809), sensu stricto.

ASTER LAEVIS L. var. **laevis** Cronquist, var. nov. *A. laevis* L. Sp. Pl. 876. 1753, sensu stricto.

ASTER PATENS Ait. var. **patens** Cronquist, var. nov. *A. patens* Ait. Hort. Kew. **3**: 201. 1789, sensu stricto.

ASTER PILOSUS Willd. var. **pilosus** Cronquist, var. nov. *A. pilosus* Willd. Sp. Pl. **3**: 2025. 1803, sensu stricto.

ASTER PUNICEUS L. var. **puniceus** Cronquist, var. nov. *A. puniceus* L. Sp. Pl. 875. 1753, sensu stricto.

Professor Fernald has recently pointed out (Rhodora **42**: 492–495. 1940) that, although northern plants referred to *A. humilis* Willd. or *A. umbellatus* var. *latifolius* Gray are merely extreme specimens of *A. umbellatus*, the southern specimens so referred belong to a well-characterized entity with larger and firmer involucres and usually broader leaves. Another character of the southern plants, not mentioned by Fernald, is so distinctive that I feel they should be specifically separated. Their heads are only 6–19-flowered, with 2–7 rays and 4–12 disk flowers. Furthermore, the general aspect of the southern plants is as nearly that of *A. infirmus* Michx. as of *A. umbellatus*, and in the character of the involucre they much more closely resemble the former than the latter. In *A. infirmus* the heads are 24–45-flowered, with 6–9 rays and 18–36 disk flowers. There is thus a clear break in number of disk flowers between the southern plants referred to *A. umbellatus* var. *latifolius*, on the one hand, and *A. umbellatus* and *A. infirmus* on the other.

A further, perhaps minor consideration is that the inclusion of these southern plants in *A. umbellatus* would remove one of the most satisfactory key-characters to distinguish that species from the universally recognized *A. infirmus*, for, while the achenes of *A. umbellatus* are hairy, and those of *A. infirmus* glabrous, those of the third group may be either glabrous or slightly hairy. The name *A. humilis* Willd. was based on northern plants which, as Professor Fernald has shown, are not separable from *A. umbellatus*. The only available specific name for the southern group, so far as I am aware, is *Aster sericocarpoides* (Small) K. Schum., based on *Doellingeria sericocarpoides* Small.

A further investigation of *Aster umbellatus* reveals that the hairy west-

ern plants which have generally been treated as *A. umbellatus* var. *pubens* Gray have a reduced number of flowers, much as in *A. sericocarpoides*. The heads are mostly 12–22-flowered, with 4–7 rays and 8–15 disk flowers, instead of 23–54-flowered, with 7–14 rays and 16–40 disk flowers. Although there is some slight failure in the distinction here, it is no greater than in many other cases of generally recognized species in *Aster*, and consistency would suggest that specific recognition is desirable. The name *Aster pubens* is preoccupied by a proposal of Otto Kuntze. Since Kuntze's name was based on a species of *Solidago*, I feel that the very similar name here proposed will cause no serious confusion.

Aster pubentior Cronquist, nom. nov. *A. umbellatus* var. *pubens* Gray, Syn. Fl. 1^2: 197. 1884.

Certain northeastern specimens of *Aster umbellatus*, chiefly from Newfoundland and Nova Scotia, have the stem, involucres, and lower surfaces of the leaves puberulent, much as in *A. pubentior* but more coarsely so. They also tend to be smaller than typical *A. umbellatus*, with fewer heads. In other respects, however, they appear to be quite typical of the species, and no clear line can be drawn to separate them. It may eventually be desired to treat them as a separate variety, but there are so many intermediates that I am not prepared to do so at this time.

The four species of *Aster* § *Doellingeria* here discussed may usually be identified by the following key.

1. Heads mostly 6–22-flowered, with 2–7 rays and 4–15 disk flowers.
   2. Involucre 3.5–5 mm. high, its bracts puberulent, generally long-triangular and acute; leaves more or less puberulent over the surface beneath; n. Mich. to Neb. and Alta. *A. pubentior.*
   2. Involucre 4–7 mm. high, its bracts glabrous or nearly so, at least the inner ones oblong or linear-oblong and obtuse or rounded; leaves usually glabrous or merely puberulent along the veins, beneath, occasionally appressed-puberulent over the surface; N. C. to Fla. and La. *A. sericocarpoides.*
1. Heads mostly 23–54-flowered, with 6–14 rays and 16–40 disk flowers.
   2. Achenes more or less strigose or puberulent; plant normally with creeping rhizomes; involucre 3–5 mm. high, its bracts relatively thin and slender; heads mostly 30–300 or more in a usually relatively dense and more or less flat-topped inflorescence, sometimes fewer in northern or depauperate forms; Newf. to n. Ga., west to Minn. and n. Ill. *A. umbellatus.*
   2. Achenes glabrous; plants without creeping rhizomes; involucre 4.5–7 mm. high, its bracts relatively broad and firm; heads mostly 5–30 in an open inflorescence, rarely as many as 75; Mass. to Ga. and Ala. *A. infirmus.*

Until the publication of the first part of the second volume of the *Genera Plantarum* in 1873, it was customary at least in America to regard the various *Aster*-segregates as valid genera. Asa Gray rather reluctantly followed Bentham's sweeping reduction of most of the segregates, and further pointed out that if these were to be reduced, *Brachyactis* would have to follow.

While the extended definition of *Aster* has certainly not been uniformly accepted, it has been followed by the majority of American taxonomists since Gray's adoption of it, more especially so since the swing away from the splitting vogue of the first quarter of this century. The Benthamian definition, with Gray's addition of *Brachyactis*, was also adopted by Hoffman in his treatment of the Compositae for the *Natürlichen Pflanzenfamilien*.

Although I do not wish to become involved at this time in a discussion of the propriety of the extended definition of *Aster*, I must support it, with some misgivings, at least until a thorough study of the old-world as well as the American species provides a reasonable basis on which all species can be referred either to *Aster* proper or to a morphologically definable segregate. (It may be mentioned that *Leucelene* might perhaps be allowed to stand without disturbing the others.)

If *Aster* is to be accepted in the extended sense, however, *Sericocarpus* must follow the other segregates to intra-generic rank. The only basis on which the several species of *Sericocarpus* might be distinguished generically is their narrow, relatively few-flowered heads. *Sericocarpus linifolius* (L.) B.S.P., the type of the genus, has 3–6 rays and 5–10 disk flowers. Another northeastern species, *S. asteroides* (L.) B.S.P., has 4–8 rays and 9–20 disk flowers. Two species of *Aster* § *Doellingeria* reach this low level, however, as noted previously: *Aster sericocarpoides* has 2–7 rays and 4–12 disk flowers and *A. pubentior* has 4–7 rays and 8–15 disk flowers. *Aster perelegans* Nels. & Macbr. (= *Eucephalus elegans* Nutt.) sometimes has as few as 4 rays and 8 disk flowers to a head. At least two species of *Aster* proper also have heads with scarcely more flowers than *Sericocarpus*. *A. parviceps* (Burgess) Mack. & Bush has 18–32-flowered heads, with only 6–14 disk flowers, and *A. depauperatus* (Porter) Fern. has 15–32-flowered heads, with 8–17 disk flowers. *Aster divaricatus* L., of the section *Biotia*, although it has more numerous disk flowers, frequently has only 5 rays.

Thus we see that a reduction in number of flowers per head has occurred in several groups in *Aster*, and that this reduction has proceeded no farther in *Sericocarpus* than in some of the other groups. All the other characters of *Sericocarpus*, including the densely hairy achenes (compare *A. novae-angliae* and *A. concolor*) and the broad, chartaceous, shortly green-tipped involucral bracts (compare *A. surculosus*, *A. gracilis*, and § *Biotia*), are within the range of variation of *Aster*. There remains no basis on which *Sericocarpus* can be segregated.

Of the two species of *Sericocarpus* in the manual range, *S. linifolius* takes the name *Aster solidagineus* Michx., since the name *Aster linifolius* is preoccupied. *Sericocarpus asteroides* apparently has no valid name in *Aster*, since the name *Aster asteroides* is preoccupied, and both *A. marilandicus* Michx. and *A. conyzoides* Willd. were illegitimate substitutes for the Lin-

naean *Conyza asteroides*, proposed at a time when the epithet *asteroides* was still available in *Aster*. Associating the species with Linnaeus, I therefore propose the name **Aster paternus** Cronquist, based on *Conyza asteroides* L. Sp. Pl. 861 (1753).

An interesting nomenclatural question might be raised as to whether the exception given in article 69 of the International Rules of Botanical Nomenclature to the otherwise blanket rejection of illegitimate names could be so construed as to make it possible to take up Michaux's name *Aster marilandicus* for the plant under discussion. The pertinent part of article 69 reads, "Where a new epithet is required, an author may, if he wishes, adopt an epithet previously given to the group in an illegitimate combination, if there is no obstacle to its employment in the new position or sense." The example given thereafter pertains to a transfer to one genus of an epithet illegitimate in another. Two competent students of the Rules have assured me that the legitimacy of *Aster marilandicus* would now be restored if I were to publish it anew, using the same type as Michaux (that is, basing it on *Conyza asteroides* L.). Another equally competent nomenclaturist has taken the stand that the provision in article 69 is meant to apply only to cases where a transfer is involved, as illustrated in the example given for it in the Rules. The point might well be considered by the next International Congress.

Professor Fernald has shown that the many-headed plant of the interior that has passed as *Boltonia asteroides* (L.) L'Hér. is not the same as true *B. asteroides* of the coastal states, and is not specifically separable from *B. latisquama* Gray. The difference between the coastal few-headed plant and the inland many-headed plant does not seem to me to be nearly so constant as Fernald makes out, however, so that all should be combined under the heading of *B. asteroides*.

Boltonia asteroides (L.) L'Hér. var. **asteroides** Cronquist, var. nov. *B. asteroides* (L.) L'Hér. Sert. Angl. 16. 1788, sensu stricto. *Matricaria asteroides* L. Mant. 116. 1767.

Boltonia asteroides (L.) L'Hér. var. **recognita** (Fern. & Griscom) Cronquist, comb. nov. *B. latisquama* Gray var. *recognita* Fern. & Griscom, Rhodora **42**: 491. 1940.

Boltonia asteroides (L.) L'Hér. var. **latisquama** (Gray) Cronquist, comb. nov. *B. latisquama* Gray, Am. Jour. Sci. II. **33**: 238. 1862.

Chrysopsis villosa is a highly variable species from which many segregates have been proposed. Some of these appear very distinct in the extreme form, but apparently all are connected by numerous intergrades.

Chrysopsis villosa (Pursh) Nutt. var. **villosa** Cronquist, var. nov. *Chrysopsis villosa* (Pursh) Nutt. Gen. **2**: 151. 1818, sensu stricto. *Amellus villosus* Pursh, Fl. Am. Sept. 564. 1814.

CHRYSOPSIS VILLOSA (Pursh) Nutt. var. **angustifolia** (Rydb.) Cronquist, comb. nov. *C. angustifolia* Rydb. Bull. Torrey Club **37**: 128. 1910.

CHRYSOPSIS VILLOSA (Pursh) Nutt. var. **camporum** (Greene) Cronquist, comb. nov. *C. camporum* Greene, Pittonia **3**: 88. 1896.

CHRYSOPSIS GRAMINIFOLIA (Michx.) Ell. var. **graminifolia** Cronquist, var. nov. *Chrysopsis graminifolia* (Michx.) Ell. Bot. S. C. & Ga. **2**: 334. 1824, sensu stricto. *Inula graminifolia* Michx. Flor. Bor. Am. **2**: 122. 1803.

When I transferred *Erigeron canadensis* L. and its allies to *Conyza*, several years ago, I accepted Robinson's treatment (Rhodora **15**: 205–209. 1913) in which he recognized the coastal *E. pusillus* Nutt. as specifically distinct from *E. canadensis*. In working over the group for the illustrated flora, I find a considerable number of intermediates. Since the plants are habitally very similar, and further since there is a chiefly western phase of *E. canadensis* which has the glabrous stem of *E. pusillus*, without sharing its other features such as the minutely purple-tipped involucral bracts, I think it is better to combine them all in one species.

All of the species which Linnaeus referred to *Conyza* in the *Species Plantarum* have now been transferred to other genera, so that the use of the name in the traditional sense can be continued only through permissive action by an international botanical congress. As noted by Bentham in the *Genera Plantarum*, the familiar application of the name was established by Lessing in his *Synopsis generum Compositarum* in 1832. The name *Eschenbachia* Moench. is available for the group, but it is relatively little-known, and only a few species have been formally transferred to it. Until the matter has been considered by a botanical congress, I intend to continue to use the name *Conyza*.

CONYZA CANADENSIS (L.) Cronquist var. **canadensis** Cronquist, var. nov. *Erigeron canadensis* L. Sp. Pl. 863. 1753.

CONYZA CANADENSIS (L.) Cronquist var. **pusilla** (Nutt.) Cronquist, comb. nov. *Erigeron pusillus* Nutt. Gen. **2**: 148. 1818. *Conyza parva* Cronquist, Bull. Torrey Club **70**: 632. 1943.

CONYZA CANADENSIS (L.) Cronquist var. **glabrata** (A. Gray) Cronquist, comb. nov. *Erigeron canadensis* var. *glabratus* A. Gray, Pl. Lindh. **2**: 220. 1850.

GRINDELIA SQUARROSA (Pursh) Dunal var. **squarrosa** Cronquist, var. nov. *Grindelia squarrosa* (Pursh) Dunal in DC. Prodr. **5**: 315. 1836, sensu stricto. *Donia squarrosa* Pursh, Fl. Am. Sept. 559. 1814.

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STATUS AND DISTRIBUTION OF CAREX NEUROCHLAENA HOLM

MAXIMILIAN G. DUMAN

Kükenthal (1909) places *Carex neurochlaena* Holm (1904) in his "species dubiae." Mackenzie (1931) regards it, together with *C. glareosa* var. *amphigena* Fernald, as a synonym of *C. marina* Dewey. But both Kükenthal and Fernald refer *C. marina* Dewey to *C. Heleonastes* Ehrh. The type specimen (*Macoun 53879*) of *C. neurochlaena* Holm, collected above Rink Rapids, Yukon River, Yukon, is preserved in the Langlois Herbarium at Catholic University, Washington, D. C. This specimen is accompanied by Holm's original drawings of the figures published with its description. Another specimen of *Macoun 53879* (isotype) in the Herbarium of the National Museum of Canada, Ottawa, is annotated by Mackenzie as "*C. Heleonastes*" (fide Porsild 1943).

The validity of *C. neurochlaena* appeared to rest on firmer ground when this species was collected at six localities in Eastern Arctic Canada by Dutilly, O'Neill and the author, and was so reported by Duman (1941). Later A. E. Porsild (1943) reported it from seven localities in the Northwest Territories, stating that its reduction to synonymy "seemed entirely unjustified," and that it "was previously known only from the type locality."

A search through the collections of closely related species in the Langlois Herbarium, the Philadelphia Academy of Science, and the Carnegie Museum, Pittsburgh, failed to reveal any additional specimens. It is significant also that *C. Heleonastes* Ehrh., which it resembles more than any other, and next to which it was originally placed by Holm, has not been reported from the arctic, while all the collections of *C. neurochlaena* are from localities with essentially arctic climates.

The following keys will help distinguish *C. neurochlaena* from related northern species.

Lateral spikes gynaecandrous, lowest spike occasionally pistillate; perigynia elliptic, 1 mm. wide, 2.5–3 mm. long, green becoming brown, subcoriaceous, attenuate at both ends; anthers 0.9–1 mm. long. *C. neurochlaena* Holm.

Lateral spikes pistillate; perigynia obovoid, 1.3–1.9 mm. wide, 2–3 mm. long, pale brown or drab, membranaceous, abruptly beaked; anthers 2 mm. long. *C. glareosa* Wahl. (var. *amphigena* Fernald).

Spikes 4–7 mm. long, few-flowered, roundish; perigynia broadly elliptic, green becoming brown, subcoriaceous, attenuate at both ends; anthers 0.9–1 mm. long. *C. neurochlaena* Holm.

Spikes 5–10 mm. long, few- to many-flowered, oblong to suborbicular; perigynia obovate, brownish-yellow, membranaceous, round-tapering at the base, rather abruptly

contracted at the apex into a short prominent beak; anthers 1.5–2 mm. long. *C. bipartita* Bellardi ex All.

Perigynia elliptic, 1 mm. wide, 2.5–3 mm. long, gradually smooth-beaked; anthers 0.9–1 mm. long; margins of the glumes clasping the perigynia. *C. neurochlaena* Holm.

Perigynia ovate, 1.5 mm. wide, 3 mm. long, abruptly scabrous-beaked; anthers 1.5–2 mm. long; margins of the glumes not clasping the perigynia. *C. Heleonastes* Ehrh.

Distribution of *Carex neurochlaena* Holm. YUKON: Yukon River above Rink Rapids, *Macoun 53879*. MACKENZIE: Mackenzie River Delta, *Porsild 2331, 2439;* Arctic Coast, *Porsild 2564, 2851;* Eskimo Lake Basin, *Porsild 2970;* Great Bear Lake, *Porsild 5031, 5115*. NORTH HUDSON BAY: Repulse Bay, *Duman 2032, 2049a1*. WEST HUDSON BAY: Baker Lake, *Dutilly 6227a;* Chesterfield, *Duman 1846, 1848, 1882b, Dutilly 6755;* Churchill, *Duman 1262, 1292, 1341, 1346, 1359, 1367;* Churchill (West of River), *Duman 1467, 1498, Dutilly 6537, 6574*. HUDSON STRAIT: Wakeham Bay, *Dutilly, O'Neill & Duman 87253*.

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ARCTIC INSTITUTE, CATHOLIC UNIVERSITY
WASHINGTON, D. C.
AND
ST. VINCENT COLLEGE
LATROBE, PENNSYLVANIA

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EUPHORBIA MACULATA L.

LEON CROIZAT

An entirely novel application of the Linnean *Euphorbia maculata* and *E. Chamaesyce* was sponsored by Wheeler (Contr. Gray Herb. **127**: 74. 1939; Rhodora **43**: 265. 1941), which aroused misgivings in the mind of prudent taxonomists. These two names had endured well over a century in a sense agreeing with current usage, and it was not certain that absolute necessity required a change.

In a previous study (Bull. Torrey Club **72**: 312. 1945), I endeavored to show that the transfer of *E. Chamaesyce* L. to a species universally known as *E. prostrata* Ait. was uncalled for, and that even a Chicagoan fragment of the "Linnean type" was not enough of a lever to effect revolutionary alterations. After the publication of this work, my advice was privately sought on whether I had objections against using *E. maculata* in the Wheelerian sense. I answered that I could not indorse this sense.

I would have stopped here, if Fosberg had refrained (Rhodora **48**: 197. 1946) from supporting Wheeler. I had felt that controversy was unnecessary because Svenson's note on *E. maculata* (Rhodora **47**: 273. 1945) gave fair warning to hopeful users of this binomial in the Wheelerian manner that they had better reinvestigate the question. It meant nothing to me that Svenson's grounds and mine were entirely different so long as the result could be the same for taxonomy.

It is clear that Fosberg is no better aware than Wheeler of the real status of the issue, which requires final restatement. The point at issue is fact, and the reader may embroider further at his own pleasure.

Boissier's monograph of the *Euphorbieae* (in DC. Prodr. **15**(2): 3. 1862) is still viable, and few taxonomists will be inclined to slight the diligence and trustworthiness of this author. Boissier's treatment of *E. maculata* (op. cit. 46) reads, "156. *E. maculata* (L. sp. pl. I. n. 21 et hb.! non L. mant.). . . . In Americâ boreali a Canadâ ad Floridam (Chapman!) et Texas! . . . . *E. supina* Rafin. dec. pl. . . . ."

It is manifest that: (1) Boissier diligently consulted the Linnean herbarium before 1862; (2) elected one particular specimen out of this herbarium as the type, which agreed with the traditional application of the binomial; (3) further investigated, reaching the conclusions that the Linnean concept of the *Mantissa* was no longer the same as that of the *Species Plantarum*.

Vague beliefs exist that the botanists of the Old World never had the perfect understanding of "type" vouchsafed to those of the New, which it

would be instructive to discuss. Whatever the details, Boissier effected in this treatment an iron-clad "typification" of the most modern pattern both under the International and the American Code of Nomenclature.

Informed of this treatment, a critical taxonomist mistrusts forthwith a photograph of the Linnean "type" of *E. maculata* disagreeing with the Boisserian understanding of it. The Linnean herbarium is well known to contain sometimes more than one specimen for the same species, and to have been handled by hands other than those of the original owner. It is also known—more or less learned discussions to the contrary—that the *Species Plantarum* is an outright compilation based upon the sexual system in lieu of a key. Discrepancies of interpretation of the "types" in the Linnean herbarium, consequently, demand a full investigation of the *entire content* of this herbarium, and the utmost caution in the application of the synonyms. Cases arise in which an old name must be sacrificed on the altar of the goddess Typification, but the sacrifice must never be allowed without question. Linnaeus had no understanding of the interspecific limits of petty *Chamaesyce* forms, and it would be a mistake to lightly prefer his judgment—if any—to that of Boissier.

The Arnold Arboretum has a complete set of microfilms covering the Linnean herbarium, and these reproductions have been properly enlarged and made available for immediate reference. The enlargements fall short of the perspicuous details apparent in other photographs of classic material from European herbaria, but are good enough, nevertheless, for the current purposes of taxonomy.

These microfilms and their enlargements prove that the Linnean *E. maculata* rested in origin upon two specimens, as follows.

(1) The specimen seen by Boissier, and indeed very well agreeing with Fosberg's *E. supina* Raf. (op. cit. 198, fig. 2); the holotype of this I have studied, bringing of it a fragment, the kind gift of Prof. H. Humbert of Paris, to the herbarium of the Arnold Arboretum. This specimen (No. 630.11 in Savage's "Catalogue") is inscribed "*21. maculata*" in an handwriting which is to all appearances Linnaeus' own.

(2) The specimen, a photograph of which was handed to Wheeler as the "type," and is mistakenly reproduced by Fosberg as such (op. cit. 199, fig. 4.). This photograph is of a plant in the vicinity of the form currently understood as *E. Preslii* or *E. brasiliensis*, and is inscribed in different handwritings both "*maculata*" and "*hypericifolia.*"

I much regret that the Linnean herbarium was not open for study when I visited London at the end of 1938, and will not venture to commit myself to certain identification of, or notes about, these plants, the intangibles of which must be studied upon the actual sheets. I am safe in the belief, nevertheless, that Boissier, who knew *Euphorbia* and studied the Linnean "types,"

in choosing one fully agreeing to sound practice was not wrong in identifying *E. maculata*. In short, Wheeler and Fosberg, unknowingly despite Boissier's outspoken warning, are trying to do in 1939, 1941, and 1946 what Boissier did in 1862, and to do it against Boissier's prior understanding. This cannot be done, and on this the matter rests.

It is consequently proper to affirm the following synonymy,

Euphorbia maculata L. sensu Boissier in DC. Prodr. **15**(2): 46. 1862. Syn. *E. supina* Raf.; Wheeler, Contr. Gray Herb. **127**: 76. 1939; Fosberg, Rhodora **48**: 197. 1946.

Considering the narrow scope of this note, I see no reason to complicate matters with a reference to *Chamaesyce*, which I emphatically hold to be the correct generic name for the group to which *E. maculata* and *E. Chamaesyce* belong.

THE ARNOLD ARBORETUM, HARVARD UNIVERSITY
JAMAICA PLAIN, MASSACHUSETTS

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THE ROLE OF CERTAIN ENVIRONMENTAL FACTORS IN GROWTH AND REPRODUCTION OF PHOTOSIPHON BOTRYOIDES KLEBS—III. REPRODUCTION[1]

SISTER M. LAURENCE MAHER, I.H.M.

Klebs (1896) and Moewus (1933) (table 1) emphasized the important role of physical and chemical factors in stimulating reproduction of *Protosiphon*. Klebs' work, however, was probably based mostly upon studies of impure (unialgal) cultures. Pringsheim and Ondraček (1939) have been unable to confirm portions of Moewus' work.

FACTORS INFLUENCING GAMETE PRODUCTION—PHYSICAL FACTORS

A. Temperature. In order to test the effect of temperature on gamete formation, a loopful of material grown on agar was transferred to each of several depression slides or watch glasses. Both depression slides and watch glasses were kept in moist chambers in covered Petri dishes. Table 14 lists data that are typical of the results obtained when the material is transferred to water. Four depression slides with thalli grown for two weeks on 0.06 per cent Bristol's solution solidified with 1 per cent agar were used for each set of temperature conditions.

Heat always acted as a stimulus to gamete formation. In unheated material, the process was slower in beginning and continued for days, particularly if the dishes were standing at a temperature below 20° C. Keeping dishes at a temperature of 28–32° C for one-half to one hour and then returning them to room temperature (18.5° C) had an effect on gamete formation similar to keeping dishes with plants immersed in liquid at a temperature a few degrees lower for a longer period. Temperatures of 28–32° C were usually more effective when they were used for one-half to two hours than when they were used for longer periods. An increase in temperature of 5–10° C above that at which the plants were grown always brings about gamete formation when plants that are at least two weeks old are immersed in water.

B. Age of Material. Material 2–12 weeks old was used for experiments on gamete formation. It was taken from cultures in which the sacs were in vegetative condition and also from cultures in which the sacs contained coenocysts, both red and green. The formation of gametes appeared to be

[1] Part I of this series appeared in Bull. Torrey Club **73**: 573–587; Part II in **74**: 20–37. Several of the tables and figures herein cited are found in Parts I and II; the summary and list of literature cited in Part III refer to the entire series.

a little slower from red coencysts, but essentially the results were the same in so far as the age of the plants was concerned.

C. Concentration of Solution. One loopful of material from clone 6*B*1 grown 37 days on 0.06 per cent Bristol's solution in 1.5 per cent agar (pH 5.7) was transferred to each of four depression slides containing 0.06 per cent Bristol's solution. A similar series of depression slides with 0.25 per cent Bristol's solution was set up. Six hours later, more gametes were observed on the slides with 0.25 per cent Bristol's solution than in those with less concentrated solution. The next morning gametes were very numerous on all the slides. Two days later, however, there were more zygotes and fewer

TABLE 14. *Effect of temperature on the rate of gamete formation in clone 8B1.*

Temperature	No. hrs. required for gamete formation	Observations
18.5° C (control).	8	Gametes came out in sticky bunches.
28° C for one hour then 18.5° C.	4	Gametes from the same sac stuck together. More motile forms than in those not heated, but the same sticky appearance.
29° C for one hour then 18.5° C.	4	Some motile forms after four hours. Gametes much more numerous, after twenty-four hours, than in either of the above.
29° C for four hours, then 18.5° C.	4	Gametes less numerous after four hours than in the dishes that were heated for one hour. After two days, also, gametes were less numerous than in dishes heated for one hour.
30° C for four hours, then 18.5°C.	4	Gametes very numerous after four hours. After twenty-four hours, gametes were less numerous than in the other heated dishes.

vegetative sacs on the slides with 0.06 per cent Bristol's solution. In 0.25 per cent Bristol's solution, zygotes were less numerous, and the proportion of sacs that had not formed gametes was greater than in the more dilute solution.

A loopful of vigorously growing vegetative thalli was transferred to depression slides in triplicate. The groups of depression slides contained respectively distilled water, 0.06, 0.12, 0.25, 1.0, and 2.0 per cent Bristol's solution. At the end of four and one half hours, gametes were numerous on the slides containing distilled water. They continued to be more numerous in this series than in any of the others during the first 24 hours. After 48 hours, motile gametes were no longer present. The contents of sacs that had

not formed gametes were still in vegetative condition. In 0.12 and 0.25 per cent Bristol's solution, after four and one-half hours, gametes were fewer than in distilled water. The process continued for a longer time than in the more dilute media and motile forms were still numerous after 48 hours. In 0.5 per cent Bristol's solution, no gametes had been discharged after four and one half hours, conjugating gametes were numerous after 24 hours, but there were none after 48 hours. In 1.0 per cent Bristol's solution, some of the sacs formed gametes, but they were not motile and none was liberated at any time during the period of observation. The contents of some of the larger sacs formed coenocysts. In 2.0 per cent Bristol's solution, no gametes were produced; after 24 hours, all the larger sacs and many of the smaller ones contained coenocysts.

D. Effect of Light on Gamete Formation. It has been noted many times in the course of the work that cultures on agar very frequently contained gametes on the day following their removal to a region of weaker illumination. Subsequent experiments indicate that weaker illumination stimulates gamete formation. Thalli from clone 6*B*1, grown for 37 days on 0.06 per cent Bristol's solution in 1.5 per cent agar, were used to test the effect of light on gamete formation. Light of three varying degrees of intensity was tested: bright light, six inches from a 300-watt water-cooled lamp, diffuse light from a north window with translucent glass, and darkness. The temperatures were similar throughout. Four depressions on slides with distilled water were employed for each light source. After four and one half hours, gametes were very numerous on the slides in diffuse light, in bright light gametes were less numerous than in either diffuse light or in darkness, and many more gametes were produced in darkness than in either of the other series. No differences were observed when experiments were begun at different times of day. Vegetative sacs of clone 7*B*2 transferred to liquid at 1:00 p.m. under identical conditions formed numerous gametes in four hours just as did those transferred at 9:00 a.m.

FACTORS INFLUENCING GAMETE PRODUCTION—CHEMICAL FACTORS

A. Effect of pH on Gamete Formation. The hydrogen-ion concentration at which material was previously grown apparently had no effect on the formation of gametes when the thalli were transferred to liquid. For example, material of clone 6*B*1 grown sixteen days on 0.06 per cent Bristol's solution in 1.5 per cent agar and with pH values of 4.1, 5.1, 6.3, 7.1, and 9.0 was transferred to series of three depression slides containing 0.06 per cent Bristol's solution at pH 4.7. After four hours at 24° C, gametes were present in all the slides. Twenty-four hours later conditions in all the dishes were the same as to motility, numbers of gametes, etc., indicating that the hydro-

gen-ion concentration of the media in which the plants were grown had no effect on rate or abundance of gamete formation.

The pH of the liquid to which the plants were transferred did, however, have a marked influence. Plants grown on 0.06 per cent Bristol's solution at pH 3.6 in 1.5 per cent agar were transferred to 0.06 per cent Bristol's solution at pH 3.6. At a temperature of 23° C gametes were present five hours later, but the harmful effect of the medium on the gametes was soon apparent. They did not show the usual prolonged motility, but rounded up at once and sank to the bottom of the slides around the sac from which they had been liberated. After ten days, there were a number of zygotes in the slides, while many partially fused cells that had not formed walls were disintegrating.

Some of the same material was transferred to depression slides with Bristol's solution at pH 5.1. Here gametes were much more numerous and motile than in the more acid solution, but there were also some disintegrating cells.

Thalli from clone 6*B*1 grown for seventeen days on 0.06 per cent Bristol's solution at pH 5.0 were immersed in distilled water and in 0.06 per cent Bristol's solution at pH 4.1, pH 7.0, and pH 9.2, at 24° C and at 27° C. Four depression slides were employed for each experimental condition. After four hours, gametes were present in all the slides. In each medium, they were more numerous on the slides kept at 27° C than on those at the lower temperature. Fewest gametes were present at pH 9.2 and most at pH 7.0 where they were so numerous that the medium appeared green after four hours.

B. Effect of Organic Media on Gamete Formation. Plants grown for six weeks on 0.06 per cent Bristol's solution were transferred to depression slides containing distilled water, 0.06 per cent Bristol's solution, 1, 5, and 10 per cent sucrose, and stored at 27° C. After five hours, gametes were present in all the slides. Gametes in 1 per cent sucrose were less numerous than in water or 0.06 per cent Bristol's solution, but more numerous than in the higher concentrations of sucrose. After 24 hours, gametes were more numerous in 1 per cent sucrose than in any other medium. After 48 hours, zygotes were more numerous in 1 per cent sucrose than in inorganic media, and there were no disintegrating cells on the bottom of the slides as there were in those containing distilled water. Just as in inorganic media, gametogenesis continued for longer time in the higher concentrations of organic media, and motile forms were still present in 5 and 10 per cent sucrose after 48 hours.

PRESENCE OF A PYRENOID

Presence or absence of a pyrenoid in the gamete was one of the characters used by Moewus (1935b) to distinguish the different races with which

he worked. He states that in the *B* race, a pyrenoid is present when gametes are formed in organic medium; lacking when they are formed in inorganic medium; and present in some and lacking in others when an organic substance is added to an inorganic medium.

Gametes shown in figure 39 were produced in 1 per cent sucrose. It can be seen that some have pyrenoids and others do not. The same observations were made when gametes produced in water or in 0.06 per cent Bristol's solution were stained with iodine. In the *S* race, likewise, pyrenoids were observed in some and not in others regardless of the nature of the medium. Gametes from the *M* race produced in both organic and inorganic media were stained with iodine, but no pyrenoid was ever observed. Gametes from the *N* race produced in water (fig. 15) contained darkly staining inclusions when treated with iodine and a pyrenoid was observed in some of them. Gametes from the *V* race produced in 0.06 per cent Bristol's solution with 0.5 per cent inulin also contained a number of darkly staining inclusions. Some contained pyrenoids. These observations on the pyrenoid of gametes do not confirm those of Moewus.

FACTORS INDUCING CONJUGATION

Zygotes were not observed inside the sacs except in the *V* culture (fig. 16), but they were obtained repeatedly when single sacs in a suitable stage of development were transferred singly to distilled water in depression slides. (They were continually present in all the clonal cultures.) For example, four single sacs from clone 7*B*2 were transferred separately to depression slides and kept at a temperature of 18.5° C; conjugating gametes were present the next day and four days later zygotes were observed. Similarly eight sacs from clone 8*B*2 were transferred singly to depression slides with distilled water at a temperature of 19° C. One day later, zygotes were observed on all the slides. Three sacs of 6*B*1 were transferred singly to drops of water on agar. Three days later zygotes were present in each drop. These experiments indicate that the *B* race is homothallic. Tests with single sacs from other races were not made, but the presence of zygotes in all the clonal cultures indicates that they also are homothallic.

Temperature. Zygotes were found in all the cultures where there was sufficient water for the gametes to swim. As a rule, slides that had been subjected to preliminary changes in temperature contained more zygotes than those kept at constant temperature. For purposes of comparison, counts were made of the number of zygospores on five or more fields and the average number recorded. Temperatures up to 34° C were used without inhibiting copulation. In some cases, more zygotes were produced when heat was ap-

plied for a shorter interval than when the dishes were kept at a higher temperature for a longer period (table 15).

An exact count of zygotes is impossible because they are present in all stages of development and cannot be readily distinguished from non-motile unfused gametes until they are mature (fig. 40).

TABLE 15. *Effect of temperature on zygote formation in clone 6B3.*

Temperature	Average number of zygotes per field three days later
14.5° C (control).	10
34° C for one hour, then 14.5° C.	30
34° C for one half hour, then 14.5° C.	40
30° C for one hour, then 14.5° C.	20
30° C for one half hour, then 20° C.	25
30° C for one half hour, then 14.5° C.	30

Even when material was kept at constant temperature zygotes were frequently very numerous. Plants two weeks old from clone 6*B*1 were transferred to distilled water in four depression slides and kept at a temperature of 18.5° C; a similar series of depression slides with material from the same culture was kept at 20° C. After three days, practically all the cells present in both series of slides were zygotes. Zygotes may be very numerous also on solid media. They were extremely numerous on 1 per cent agar in Petri dishes two days after the cultures were inoculated with clone 6*B*1. The temperature was 23.5° C.

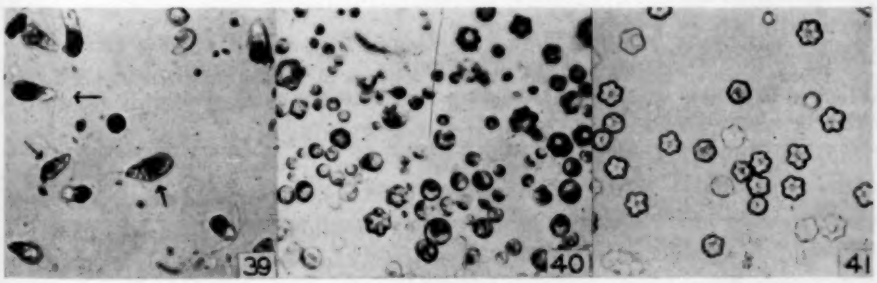

FIG. 39. Gametes from clone 2*B*1 24 hours after thalli were transferred to 1.0 per cent sucrose solution. ×675. The cells were stained with dilute iodine solution; arrows indicate cells showing pyrenoids. Some cells show three of the four flagella indicating that fusion of gametes has taken place. FIG. 40. Zygotes from clone 6*B*3 three days after thalli were transferred to depression slides with water. They were kept at 30° C for one hour and then at 20.5° C. ×350. FIG. 41. Zygospores from clone 6*B*1 ten days after thalli were transferred to depression slides. ×350.

Ability to copulate was not lost when the temperature was lowered. A culture of clone 7*B*2 was kept for 16½ hours at a temperature of 33° C. Some

thalli were then transferred to water in depression slides and kept at 6° C for four hours and then at 16° C. Another series from the same culture was kept at 16° C; in both series copulating gametes were numerous after 24 hours.

Material of the same age (two weeks) from clone 8*B*2, not previously treated with heat, was placed in watch glasses and exposed to a temperature of 33° C for four hours, then stored at 16° C. Copulating gametes were fairly numerous after 24 hours and zygotes were very numerous after three days.

Light. Zygotes were formed both in light and in darkness. It was not determined with certainty whether or not one was more effective than the other in this respect. In the experiment on the effect of bright light, diffuse light, and darkness described previously, zygotes appeared to be more numerous in the slides stored in bright light than they were in the others. In similar experiments, however, no significant difference in the relative numbers of zygotes was observed. Light is not essential to the formation of zygotes, inasmuch as they were observed in cultures that had been kept in total darkness for three months.

Concentration of Medium. Zygotes were produced in greater numbers in less concentrated solutions. When 0.06, 0.12, 0.25, and 0.5 per cent concentrations of Bristol's solution were used, zygotes were most numerous in 0.06 per cent Bristol's solution. When 0.06, 1.0, and 2.0 per cent concentrations of Beyerinck's solution were used, zygotes were also much less numerous in the higher concentrations.

TABLE 16. *Effect of pH on the formation of zygotes in clone 6B1*

Plants growing in 0.06 per cent Bristol's solution in 1.5 per cent agar at pH 5.0 for seventeen days were transferred to 0.06 per cent Bristol's solution with pH adjusted to the values indicated.

pH	Temperature	Number of zygotes per field two days later
Distilled water	24° C.	25
4.1	24° C.	5
4.1	27° C.	20
7.0	24° C.	12
7.0	27° C.	15
9.2	24° C.	40

High concentrations of sucrose were found less effective in stimulating the production of zygotes than 1 per cent solution. Zygotes were more numerous however in 1 per cent sucrose than in distilled water or 0.6 per cent Bristol's solution when all other conditions were identical.

Hydrogen-ion Concentration. Zygotes were very numerous both in liquid and on agar for all the pH values that were observed in this connection. They were unexpectedly numerous on agar at pH 3.6, a hydrogen-ion concentration so far from optimum that there was no growth when the solution was used in liquid form.

When sacs grown on agar were transferred to groups of four depression slides with 0.06 per cent Bristol's solution at various pH values, the number of gametes that initiated fusion but dropped to the bottom and disintegrated was greater in acid than in basic media. This may account for the higher number of zygotes observed in basic media (table 16).

The large number of fusing cells at pH 4.1 that disintegrated without forming a cell wall indicated that this solution was unfavorable for good development of gametes. Figure 41 shows zygotes from the solution at pH 9.2, ten days after the slides were prepared.

DISCUSSION

Protosiphon botryoides is not so favorable an organism for quantitative study as such an alga as *Chlorella*. The latter possesses such advantages as more homogeneous cell size and distribution through the culture medium, both of which are absent in *Protosiphon*. The tendency of some cells of *Protosiphon* cultures to form gametes readily during the experimental period (owing, perhaps, to micro-environmental differences), while others continue to grow as vegetative individuals, renders attempts to secure quantitative data more difficult. This is further complicated by the fact that the developing plants are often crowded together in portions of the culture dishes as a result of the phototactic responses of the gametes, so that the ultimate size attained by individual cells is probably influenced by intercellular competition. In spite of these difficulties it seemed desirable to obtain quantitative data from the experiments, especially because of Moewus' rather categorical conclusions as to the influence of various environmental factors. To this end such criteria of growth were employed as mean size of 100 sacs per culture, density according to arbitrary color standards and amount of centrifugate. In the light of the difficulties mentioned above, the results obtained from such analyses are at best approximations.

The races of *Protosiphon* available for the present study were isolated from soil from New York, N. Y. (*B* race); Pennsylvania (*M* race); Virginia (*V* race); Nebraska (*N* race); and Syracuse, N. Y. (*S* race).

Cultures from the *B* and *M* races have been grown side by side at various temperatures in both organic and inorganic media for more than three years. Under the most favorable conditions, the length of sacs from the *M* race is from one-fifth to one-fourth that of the *B* race. Iyengar (1933) described

an Indian form that he calls *Protosiphon botryoides* Klebs forma *parieticola* f. nov. It was found on the walls of houses and compounds where droppings of birds and other organic matter were present during the monsoon season. He reports that plants near the bottom of the wall where conditions were more favorable had a short rhizoidal portion and resembled *Chlorococcum* and if it were not for the series of transitional forms might be mistaken for that genus. Under less favorable conditions, cells of the *M* race also lack rhizoidal portions and resemble *Chlorococcum*. The dimensions given by Iyengar are not significantly different from the corresponding dimensions of plants from the *M* race, as is apparent from the following data:

Sacs from	*Length*	*Width*	*Diameter of coenocysts*
Indian form	0.2 mm.	0.07 mm.	0.018–0.3 mm.
M race	0.15 mm.	0.04 mm.	0.015–0.078 mm.

In both forms, the smaller sacs frequently form one large coenocyst. Iyengar says that one gamete of a fusing pair is frequently larger than the other. In the *M* race some gametes were twice as large as others..

A desert form of *Protosiphon* was discovered by Nayal (1933) and called by him *Protosiphon botryoides* (Kutz.) Klebs var. *deserti*. The average size of the plants (1.25–1.6 mm. long and 0.13–0.18 mm. broad) is approximately the same as that of the *B* race. The difference seems to be in the gametes which are described as fusing in an end-to-end position without first becoming laterally apposed. He reports that the gametes are isogamous, but that those from the same mother-cell do not fuse, i.e. this race is heterothallic. Some of Nayal's illustrations of "compound" swarmers are very similar to forms commonly seen in cultures of the *M* race. He interprets them as masses of two or more swarmers which did not separate before escaping from their mother cells. He reports that some of them separate while swimming, and that others behave as asexual zoospores. Klebs (1896) also reports fusion of more than two gametes. The large and peculiarly shaped zygotes from the *V* race (fig. 17) appear to have been formed from more than two gametes.

The zygospore is unfavorable for cytological study (Bold 1933), but such study would doubtless shed much light on the role played by "compound" forms in the life cycle of the organism.

Except for the peculiar budding from the top of cells in the *V* race (fig. 13), which was not seen in the other races, the *N*, *V*, and *S* races are very similar to the *B* race.

The use of an artificial light source for growing cultures of algae produces uniform results and is used by many modern investigators (Bold 1942; Pringsheim 1946). However, cultures kept for three months in total darkness showed considerable growth. This also is in agreement with the findings

of other investigators. Beyerinck (1898) described the growth of *Chlorella, Scenedesmus*, and other algae in total darkness and concluded that the nutrition of such forms may be either autotrophic or saprophytic depending upon the composition of the medium. Dangeard (1933) found that cultures of *Scenedesmus acutus* maintained their green color after eight years in total darkness. Meyers (1940) used a photoelectric spectrophotometer to observe the pigments of *Chlorella* and other algae that were grown in darkness in organic media. He could detect no difference between pigments produced in darkness and those produced in light. Bristol-Roach (1928), working with *Scenedesmus*, found that the addition of sugar increased the growth in light as well as in darkness, and concluded that normal photosynthesis and assimilation of sugar may be carried on independently and simultaneously by soil algae, and that growth in the lower layers of the soil is at the expense of organic matter in the soil. According to Ruben and Kamen (1940) the chief difference between photosynthetic and non-photosynthetic reactions is the fact that the former obtain energy from light and are endothermic and the latter obtain necessary energy from exothermic reactions.

The experiments with *Protosiphon* indicate that the amount of material needed to supply energy is very small, inasmuch as the only organic material available in some liquid cultures where considerable growth occurred was the small amount apparently transferred with the thalli when the inoculations were made. On slants, there was more growth than in liquid media because of the organic matter available from the agar (Robbins 1940).

The concentration of agar in various media (table 7) markedly influences cell size as Moewus (1933) also observed. The longest sacs after 24 days growth in 0.06 per cent Bristol's solution with various concentrations of agar were produced on slants with 0.5 per cent agar. In Pringsheim's solution, however, the longest sacs occurred at an agar concentration of 0.75, 1.0, and 1.5 per cent. The average length of sacs on these three concentrations was the same. Moewus (1933) stated that 0.7 per cent agar was the optimum concentration for solidifying nutritive media for growing *Protosiphon*. Cells from liquid media tend to remain spherical (figs. 22, 33) while the same media solidified with low concentrations of agar (0.5–1.0 per cent) stimulate growth of the rhizoidal portion (fig. 23). This is undoubtedly correlated with the natural habitat of *Protosiphon* on soil, and probably is a manifestation of both positive thigmotropism and phototropism.

The composition of Pringsheim's solution differs considerably from that of Bristol's solution, and in most cases the length of the sacs was less in Pringsheim's solution (table 7), but the form of the plotted curve was the same. This is an indication that the difference in results was not due to difference in composition.

Although length of sacs is not a reliable criterion for amount of growth in liquid media, nonetheless it appears to be significant that in four of the six media listed in table 6, sacs grown in solution with a concentration of approximately 0.06 per cent of nutrient salts are longer than those grown in higher concentrations. A concentration of 0.06 per cent was accordingly used for all cultures except those used for testing the effect of concentration.

The data summarized in table 6 agree with the expectation that, inasmuch as *Protosiphon* is found so universally in soils, it must be capable of growing on nutrient materials rather widely distributed and under varying conditions. Results with Beyerinck's solution were variable. In table 6, the total yield of centrifugate from this solution was small. In the experiment designed to compare equal concentrations of different media, the yield was good. The principal difference between this and other media used is that the proportion of potassium is less. Reed (1907) states that cells of *Spirogyra* elongate but do not divide when potassium is lacking in the nutrient solution. The low final hydrogen-ion concentration of the solution no doubt has an effect on the results obtained. Hoagland (1944) emphasizes the role played by potassium in plant buffer systems.

In the three culture media used for studying the effect of different NO_3/NH_4 ionic ratios (tables 8, 9) the largest sacs were produced in the cultures with nitrate nitrogen only. In all three after 24 days growth, the smallest sacs were found in the cultures with ammonium nitrogen only. Cultures on Bristol's solution with ionic ratio 50 NO_3/50 NH_4, at the end of 24 days were in vegetative condition, indicating that they were still growing. The yield from flasks with medium in liquid form was also higher than from any of the other liquid media. The presence of well developed sacs (fig. 31) was a further indication that this medium was favorable to good growth.

In Pringsheim's solution, factors other than nitrogen source had a bearing on the results: in Bristol's and Detmer's solutions, most of the sacs in cultures with nitrate nitrogen contained coenocysts and increase in thallus size had ceased; in Pringsheim's solution with nitrate nitrogen, on the contrary, the sacs were still in vegetative condition and consequently capable of growing longer. In Pringsheim's solution with ionic ratio 50 NO_3/50 NH_4, a precipitate was present that may have removed needed ions from the solution, thus inhibiting growth.

The hydrogen-ion concentration of Detmer's solutions with the lower NO_3/NH_4 ratios was already too low for good growth when the solutions were inoculated, and it dropped still lower, indicating that with the absorption of ammonium ions, OH ions were also being removed from solution. The appearance of cells from liquid cultures indicated that the solutions were unsuitable for good growth. Trelease and Trelease (1933, 1935) emphasized the advantages of employing solutions in which the proportions of nitrate

and ammonium nitrogen are physiologically balanced so that under the influence of absorption and excretion of substances by the plant, hydrogen-ion concentration would tend to remain constant.

Pringsheim (1946) states that delicate algae which lose their fresh color in solutions containing nitrate or ammonium salts only, or in those containing ammonium nitrate, may be reared successfully in media with nitrogen supplied by two different salts. Chu (1942) concluded that planktonic algae with few exceptions grow equally well in media with nitrate and those with ammonium salts as long as the nitrogen concentration is within the optimum range.

For about seventy-five years, it was assumed that only ten elements were indispensable for the growth of the higher plants. Refinement of methods in recent years has made it possible to prove that other elements in addition to the traditional ten are needed. Hoagland (1944) states that the necessity for boron and manganese has been demonstrated by many investigators and accepted by all. Evidence for the need of copper and zinc is less extensive, partly in the case of copper at least, because of the difficulty of excluding the small amount of the element in the form of impurities. Both elements are included in the list of essential element by Hoagland (1944).

Lipman (1940) notes the dire need for many more investigations of the chemical elements needed by microscopic plants. Studies that prove elements essential for higher plants do not necessarily prove that the same elements are needed by lower plants. Pringsheim (1946) states that the fact that much more is known concerning nutrient solutions for higher plants shows that there is still a wide and promising field of investigation with respect to the algae. Bold (1942) found that micrometabolic elements are undoubtedly important in the nutrition of algae and recommended that they be included in all culture solutions in spite of the possibility of their introduction as impurities in other salts.

A minor element solution containing the four elements mentioned above has been used by Craig and Trelease (1937) for the culture of *Chlorella*. It was found that the addition of very small amounts (approximately 0.007 ppm. of B, 0.0003 ppm. of Cu, 0.01 ppm. of Zn, and 0.02 ppm. of Mn) to the undiluted culture medium produced results that could be readily seen and measured.

In 1939, Arnon and Stout showed that tomato plants grown in purified solutions with eleven essential elements developed deficiency symptoms that could be prevented by adding one part of molybdenum to 100,000,000 parts of nutrient solution. Steinberg (1937) demonstrated that molybdenum is required by *Aspergillus niger* to a greater degree when nitrate is the source of nitrogen than when ammonium or organic nitrogen is supplied. In the present study it was found that 2 ml. of molybdic acid solution added to

0.25 per cent Bristol's solution (1 to 250,000,000 parts of nutrient solution) gave an increase in growth that could be seen and measured.

Moewus (1935a) reported that he obtained good growth of *Protosiphon* in solid media with a pH range of 4.5–9.5. The present experiments in general confirm this, but at the same time indicate that *Protosiphon* is more tolerant of media with low pH values when the latter are solidified with agar. The increase in growth observed in this and in other experiments when media is solidified with agar may indicate an adsorption of certain ions by the agar, but it seems more probable that the explanation given by a number of investigators in growth of fungi applies here. Fries (1938), Leonian and Lilly (1940), Robbins (1940, 1941), and others observed that the amount of growth was greater in a medium solidified with agar than in the same medium used in liquid form. They attribute the difference to presence of growth substances in the agar and in some instances demonstrated specific growth substances responsible for the results.

On acid media, sacs and coenocysts were formed more quickly than on media that were more nearly neutral, but the plants did not become so large. This is in accord with the conclusions of Artari (1913), who found that *Chlamydomonas* grows faster at first in an acid medium, but that ultimately the amount of the growth was the same when a more alkaline medium was used. Pringsheim (1926a) recommends neutral or slightly alkaline media as most favorable for most algae. In the experiments with *Protosiphon* it was found that media with pH values ranging from 4.5 to 8.5 gave good results in both liquid and solid media. On solid media, good growth was secured throughout the range used (pH 3–9.5). In liquid there was no growth in cultures with pH values lower than 3.6.

Moewus (1935a) used cultures with pH values from 4.5 to 9.5, but Pringsheim and Andraček (1939) obtained growth of *Protosiphon* only between pH 5.5 and 8.0. They report that plants were decolorized in basic solution and remained green for some time in acid solution with a pH value lower than 5.5, but did not grow. The present study confirms Moewus' results in this connection.

Growth in media with various hydrogen-ion concentrations evokes considerable variation in form. In acid media sacs elongate very readily in either liquid or solid substrata, and are characterized by a club-shaped green portion and a colorless rhizoidal portion. In the more alkaline solutions, the cells remain spherical in liquid and in some cases, sacs growing inside a spherical mother cell have the appearance of colonial forms (fig. 33).

The calcium requirement of *Protosiphon* was investigated in connection with the preparation of solutions with different pH values. In some of the alkaline solutions the calcium compound caused the formation of a precipitate. In some cases, the presence of a precipitate did not interfere with

growth, but in others it appeared to inhibit it. It was found that good growth could be obtained when calcium was omitted from the culture medium. This does not necessarily mean that no calcium was present, however. Magnesium compounds were included in all the formulae used. Mast and Pace (1939) analyzed by means of spectrograms a number of the purest magnesium salts that could be obtained and found that calcium was always present as an impurity. Chu (1942) states that the Ca requirement for algae is lower when the Mg requirement is higher.

It is generally held that calcium is necessary for growth and reproduction of all organisms except fungi, and some flagellates and algae. Pringsheim (1926b) used sodium oxalate to precipitate calcium from media used to grow algae. He divided the algate studied into forms that did not need calcium and were not inhibited in their growth by sodium oxalate in the concentrations used and those that did need calcium and upon which sodium oxalate had a toxic effect. He made no attempt to prove total absence of calcium and states that calcium traces can be assimilated in the presence of sodium oxalate. He states (1946) that calcium should always be provided in media used to culture algae, but mostly in very low concentrations because of its tendency to precipitate phosphates and iron unless the solution is so definitely acid that it would be harmful to most species.

When *Protosiphon* was grown in 0.06 per cent Bristol's solution (table 10) with the concentrations of sodium oxalate used by Pringsheim (1926b) it was found that there was better growth in the solutions with sodium oxalate than in the controls both with and without calcium. This increase in growth obscured the effect of lack of calcium.

Mann (1932) found that the concentrations of sodium oxalate used by Pringsheim increased the growth of *Aspergillus niger* and concluded that the stimulating effect might be due either to the effect of some impurity in the sodium oxalate or to ability of the fungus to utilize carbon from the oxalate. In view of the stimulation of growth obtained when additional carbon in the form of carbohydrates is added to the medium used to culture *Protosiphon* it seems reasonable to assume that this organism also is capable of utilizing carbon from sodium oxalate.

It has been clearly demonstrated by Chodat (1913) and more recently by Hall and Schoenborn (1938) that chlorophyll-bearing algae are stimulated by the addition of organic substances to the culture medium. The addition of a number of different carbohydrates to the media used for growing *Protosiphon* resulted in an increase in the length of sacs grown on agar and in the amount of material centrifuged from flasks with liquid media. Inulin was found to be most effective in promoting growth and xylose least so. Nearly twice as much material was centrifuged from flasks with 0.5 per cent inulin as from those with 0.5 per cent dextrose. Very good growth was

obtained also with fructose. This is to be expected, inasmuch as inulin yields two molecules of fructose on hydrolysis.

Matruchot and Molliard (1902), Artari (1906), Kufferath (1921), and others have compared the effect of different carbohydrates on various types of algae. Artari (1913) discussed the conflicting reports regarding ability to grow in the dark, position of pyrenoids, and other reactions to different media, and concluded that it was possible that cultures from the same species and having the same morphology might belong to different physiological races.

Extensive experiments were not performed on the effect of proteins on the growth of *Protosiphon;* it was found, however, that very good growth was secured with beef extract and with peptone used either alone or with 0.06 per cent Bristol's solution. Pringsheim (1946) states that the usual peptones, prepared from muscle, contain sufficient mineral substances so that further additions are usually unnecessary.

The importance of the relative proportions of carbohydrates and of organic compounds has long been recognized. Artari (1906) reported that the value of different nitrogen sources depends to a great extent on the presence of glucose. He concluded that ammonium nitrate was a better source of nitrogen for *Chlorella communis* than potassium nitrate when glucose is present. Kraus and Kraybill (1918) emphasized the importance of the relative proportions of carbohydrates and organic nitrogenous compounds in the carbohydrate-nitrogen ratio in their work on tomato plants.

Vischer (1926) and Wall (1939, 1940) subscribe to a theory that deficiency of potassium affects the synthesis of protein from the simpler compounds. Hoagland (1944) states that evidence of the immediate necessity of potassium for the condensation of sugar units to form starch or other polysaccharides is insufficient, but the effects on carbohydrate metabolism and synthesis when plants are grown for a long time under potassium deficiency show that potassium plays some part in the process.

Steinberg (1939) found that admixture of carbon compounds incapable of assimilation when they were the sole carbon sources markedly increased their assimilability. He stated that *Aspergillus niger* was capable of maximum growth with inorganic nitrogen and sucrose. He interpreted the result as mutual supplementation of compounds deficient in essential molecular configurations.

These references and innumerable others that might be mentioned emphasize the complexity of problems dealing with metabolism.

Klebs (1896) and Moewus (1933, 1935a) (see tables 1 and 2) both investigated the influence of environmental factors on gamete formation. Klebs' work was based on unialgal cultures, but Moewus claims to have used pure cultures. The experiments summarized under "factors influencing gamete

production'' represent a preliminary attempt to confirm the results of these investigators. As noted by them, change in temperature has a marked effect on the rate of formation. The time required varied from four to twenty-four hours. In material transferred to liquid and then exposed for periods up to six hours to temperatures a few degrees higher than that at which the cultures had been growing, gamete formation is much accelerated, and begins sooner than in material treated identically except for change in temperature. Four or five hours treatment at a temperature of 28° C evoked lively formation of gametes from material in the coenocyst stage; at 18.5° C, from eight to nine hours were required. The present observations that short periods of increased temperature decrease the time required for gamete formation correspond with the results reported by Klebs (1896), but the temperatures here used are higher than those he found effective. He states that 24–26° C is optimum and that within these limits, two and one-half hours is sufficient time for gamete formation. At 8° C and below according to Klebs, more than nine hours are required. Moewus (1933), on the other hand, reports that at all temperatures between 7° and 28° C gametes were formed in four to five hours apparently at the same rate. Cultures one to eight weeks old grown on 0.7 per cent agar were used by Moewus. The cells were transferred from agar to tap water, distilled water, and to Kolkwitz' and other solutions. He reports that no gametes were formed at 5° C and under, or at 30° C and over, but that their formation is as rapid at 7° as at 21° C, or at Klebs' optimum of 23–26° C when the cells were previously cultivated at room temperature. No confirmation of Moewus' (1933) conclusions in this regard have been obtained in the present investigations.

When material from *Protosiphon* cultures from two to twelve weeks old was transferred to liquid for gamete formation, differences in the length of time required for the process could not be attributed to the age of the material. Gametes were produced from vegetative thalli seventeen days old in the same time required for gamete formation from red coenocysts twelve weeks old. At room temperature, the rate of gamete formation in older cultures appeared to be a little slower, but the differences in time required for gamete formation to begin in any of the experimnts with material of different ages at the same temperature were not great. The results are in agreement with those of Moewus (1933) to the extent that cultures of different ages and from different media require approximately the same amount of time for gamete formation to begin when they are put into the same medium and kept at the same temperature. Klebs (1896) found that gamete formation from red coenocysts was usually slower and required 24 hours at room temperature. In the present study, 24 hours were sometimes required when the temperature was below 18° C, but the same amount of time was required by cultures two weeks old under the same conditions.

The observation that concentration of the medium has a marked bearing on the process of gamete formation is at variance with Moewus' (1933) report but supports Klebs (1896). Gamete formation was more rapid but of shorter duration in 0.06 per cent Bristol's solution than in higher concentrations. It continued for 24 hours in 0.06 and in 0.5 per cent Bristol's solution and for 48 hours in concentrations of 0.12 and 0.25 per cent solutions. In 1.0 and 2.0 per cent conentrations of Bristol's and Beyerinck's solutions, most of the sacs had formed coenocysts after 24 hours and few if any gametes were produced in liquids with such concentrations. Klebs (1896) and Moewus (1933) reported gamete formation in 1.0 per cent nutrient solution. Klebs stagted that gamete formation was slower as the concentration of the solution increased, but Moewus (1933) includes media with a concentration of 1.0 per cent among the factors that have no effect on the rate of gamete formation.

Klebs' statement that lack of light is a stimulus for gamete formation was confirmed in the experiment with effect of light on gamete formation. Slides kept in darkness contained more gametes after four and one-half hours than those in dim light or in bright light. Moewus (1933) stated that there was no difference in rate of gamete formation in light and in darkness.

Klebs (1896) and Moewus (1933) also investigated the effect of chemicals in stimulating gamete formation and reached various conclusions summarized in tables 1 and 2. In the present study, when thalli grown on media with various pH values were transferred to 0.06 per cent Bristol's solution (pH 4.7), no difference in the rate of gamete production could be observed. When thalli grown at a given pH value were transferred to 0.06 per cent Bristol's solution with various pH values, the effect of different degrees of acidity was marked. In 0.06 per cent Bristol's solution with pH 3.6, the period of motility of the gametes was short. They appeared to round up immediately and could often be seen on the bottom of the depression slides around the sac from which they were produced. In acid media, the period of active gamete formation was shorter than in media with a reaction nearer to neutral or in alkaline media.

Moewus (1935a) reported that races of *Protosiphon* with phenotypic sex determination (homothallic) produce more + than – gametes when acid solution (pH 4.5) is used for culture and gamete formation and that there are more – than + gametes after culture and gamete formation in alkaline medium. At pH 7.0, + residual gametes are present in half the dishes and – residual gametes in the other half of the dishes. He denominated cells reacting in this way as "phenotypically dioecious" and concluded that sex was not determined during gamete formation, but during the 48 hours following gamete formation.

The classification of the *B* race (obtained by Moewus from Bold, and also

used in these studies) by Moewus (1935b) as dioecious with genotypic sex determination, and his explanation that a mutation may have taken place have already been mentioned. Bold (1933) reported that he was not certain whether or not meiosis occurs when the zygote germinates, but that by analogy with the conditions known to exist in some other forms it may do so. As authority that meiosis takes place when the zygote germinates, Moewus (1935b) cites Kniep (1928). Kniep, however, states that we cannot answer finally if *Protosiphon* has genotypic sex determination, but that it is *presumed* that such a difference is necessary for copulation, and that a reduction division *probably* takes place at or before germination.

Moewus (1935b) assumed that since reduction division occurs at the germination of the zygote, the developing plants are haploid. When the germinating zygotes reached a certain size (mostly 8-nucleate), he transferred them to the surface of agar in Petri dishes. The surface of the dishes was covered with water, and they were kept in darkness at a temperature of 28–30° C. At that temperature, according to Moewus, copulation did not take place, and the darkness kept the gametes from collecting phototactically. He transferred these individual plants developing in such cultures, and assumed they were clonal.

Bold (1933), however, points out that the uninucleate segments of thalli or coenocysts formed by cleavage are not definitive gametes, but they undergo one or two bipartitions before they become gametes. Moewus (1935b) refers to this and states that because of the nuclear divisions referred to by Bold (1933), the number of swarmers that goes out from a cell is always a multiple of two. He states that in three out of sixty-five hundred developing zygotes less than eight haploid clones were obtained because one or more gametes failed to develop. In all other cases, he states that eight haploid clones were obtained and cytological investigation always showed eight nuclei in the developing zygotes. From germinating zygotes of the *B* race he obtained four + and four – clones. He agrees with Bold (1933) that the nuclei divide before gametes are formed, but does not explain why the division of eight nuclei results in the production of eight instead of sixteen or even thirty-two gametes.

In the present study, this method of securing clones was unsuccessful, partly because it was found that a temperature of 28° C stimulates copulation. Klebs (1896) also states that a constant temperature of 26–27° C during the last phase of gametogenesis inhibits the ability to conjugate, ond reports that ability to conjugate is lost when the gametes are brought to a lower temperature. Neither of these statements could be confirmed, for zygotes were formed in temperatures up to 34° C. Slides with swarmers were frequently subjected to an increase in temperature and then returned

to a lower one without any loss in ability to conjugate. Change in temperature on the contrary appears to be a stimulus for conjugation.

In 1.0 or 2.0 per cent inorganic medium, the contents of the sacs changed to coenocysts and few if any either of swarmers or zygotes were seen. In 1.0 per cent sucrose zygotes were more numerous than in distilled water or in 0.06 per cent Bristol's solution. These results are in agreement with those reported by Klebs (1896), but not with those of Moewus (1935b) who states that copulation takes place in 1.0 per cent Kolkwitz' solution and also in a concentration twenty times higher.

No clear-cut relation between hydrogen-ion concentration and number of zygotes was observed (table 16). With all other conditions the same, change in temperature appeared to be a more important factor. On agar slants, zyogtes were more numerous when the temperature was above 22° C, regardless of hydrogen-ion concentration.

According to Moewus (1935b) + and – gametes should be formed in equal numbers by thalli from the *B* race. If the sex determination were phenotypic, according to the same author, both high temperature and acidity should combine to give an increase in the number of + residual gametes and correspondingly less conjugation. In alkaline medium there would be more – residual gametes.

No evidence of sexual dimorphism was found in the present study. Material from the *B* race was used for all the experiments with environmental factors, but zygotes were seen in all the clonal cultures of all the races studied, all of which are therefore monoecious or homothallic. In all the slides with thalli immersed in liquid and also on agar, the formation of zygotes was such a continuous process that it was impossible to determine whether the smaller cells were rounded up unfused gametes or zygotes that had not yet acquired the characteristic star-shaped wall. Pringsheim and Ondraček (1939) likewise found that the process of zygote formation was a continuous one, and were unable to secure residual gametes even when they removed motile unfused ones to distilled water in separate dishes.

Carter (1926) noted that gametes of *Protosiphon* sometimes fuse within the mother cell without being released. Klebs (1896) stated that gametes from the same mother do not, as a rule, copulate, but that zygotes are present occasionally in sacs containing coenocysts. Zygotes from the *V* race are shown enclosed in a sac in figure 16. Zygotes appear to be formed more readily in this than in some of the other races. They were often observed on depression slides to which single thalli had been transferred. In some cases zygotes were not obtained either because the temperature was not conducive to copulation or because the sacs were not in a suitable condition.

Observation of cultures under different environmental conditions provided some evidence that gametes develop directly into new thalli when all

the conditions are favorable and that some stimulus such as a change in temperature or hydrogen-ion concentration is required to initiate conjugation.

Bold (1933) has described the germination of a zygote into a thallus, and there is no doubt that this is the usual method of development. It seems possible, although the process was not observed, that gametes may sometimes be produced from zygospores (fig. 41). Empty zygospore walls were observed in a number of cultures. On the slide from which figure 41 was photographed, there were in addition to the empty zygospore walls rows of small new zygospores that were being formed throughout the 38 days that this set of slides was kept under observation. In none of the empty cells was there any evidence of degenerating cell contents.

SUMMARY

(of the entire work)

A study of the effect of controlled environmental factors on the growth of certain clones of *Protosiphon botryoides* has revealed the following:

1. Cultures grown in artificial light are more successful than those grown in natural light. Ten hours daily illumination from a 300-watt water-cooled bulb seems to be optimum.

2. In a growth period of 24 days, sacs with an average length of 0.94 mm. were secured on 0.06 per cent Bristol's solution modified by substituting 0.3 gram of K_2HPO_4 for the same weight of K_2HPO_4 in the formula, thus obtaining a pH value of approximately 6.3. Minor elements solution was added to the medium which was congealed with 0.5 per cent agar.

3. Agar concentrations of from 0.5 to 1.5 per cent are optimum for normal growth. Larger sacs were developed on solid than in liquid media. After 24 days, the longest sacs (0.94 mm.) occurred in 0.06 Bristol's solution with 0.5 per cent agar. After 40 days, the longest sacs (1.3 mm.) developed on 0.06 per cent Bristol's solution with 1.5 per cent agar.

4. *Protosiphon* grows readily in a number of different media commonly used for the cultivation of algae. In inorganic media, a concentration of 0.06 per cent by weight was more satisfactory than either higher or lower ones.

5. The largest sacs were formed at a continuous temperature of 17° C.

6. The addition of 0.25 per cent inulin to inorganic media increased the amount of growth more than does the addition of any other carbohydrate. The addition of 0.25 per cent glucose increases the amount of growth in light and effects good growth in darkness.

7. Pyrenoids are present in some gametes from the *B* race and not in others, whether they are produced in inorganic or organic or both types of nutrients.

8. In acid media (pH 3.4–6.9) sacs are formed more luxuriantly than in basic media. In the more alkaline media used (pH 8.4–9.5) most sacs remained spherical in shape and were not differentiated into the club-shaped green portion and the clear rhizoidal portion in the substrate that is characteristic of plants growing in acid media or in nature.

9. Sacs with lobes and branches are of much more common occurrence in acid than they are in basic media.

10. On solid media, there was good growth in media with pH values ranging from 3.0 to 9.5. In liquid media, there was growth from pH 4.1 to 9.6. Media with pH values from 6.0 to 7.0 are optimum.

11. Nearly all solutions in which *Protosiphon* was grown changed toward a neutral hydrogen-ion concentration whether they were originally acid or alkaline in reaction.

12. The amount of calcium present as impurities in the salts used to make up culture media is sufficient for good growth of *Protosiphon*. Growth is excellent in solutions containing sodium oxalate, probably because of utilization of the carbon rather than because of absence of calcium.

13. Increase in temperature hastens the formation of gametes. Exposure of cultures grown at 17–20° C to temperatures of 24–31° C for periods of one-half to four hours results in the production of gametes in from four to six hours.

14. Zygotes were present in all the clonal cultures studied. The clones available are therefore homothallic. Zygotes are produced in temperatures as high as 34° C.

15. Zygotes are more numerous in inorganic culture media at 0.06 per cent concentration than at concentrations of 1.0 or 2.0 per cent.

16. No sexual dimorphism was found, and all the swarmers appear to be capable either of developing immediately into vegetative plants, or of fusing to form zygotes.

BIOLOGICAL LABORATORY, FORDHAM UNIVERSITY
NEW YORK

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BULLETIN OF THE TORREY BOTANICAL CLUB
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TORREYA

Plant Hormones[1]

P. W. Zimmerman

I have chosen to talk to you about a comparatively new subject, "plant hormones."

To show the growing interest in the subject, I recall that in 1935 when the A.A.A.S. met in St. Louis only five papers were presented on the subject of growth substances. At the meeting just concluded in Boston more than 25 per cent of all papers in Plant Physiology were on some phase of plant growth-regulating substances. In the American Society for Horticultural Science meetings 11 of 12 papers presented on Sunday morning involved plant hormones. In the section on Floriculture and Ornamental Horticulture 5 of 11 papers concerned plant hormones. Several papers presented in the General Section were on this subject. The line of approach varied from highly theoretical to factual information and practical applications.

In 1935 much attention was given to curvatures of stems, epinasty of leaves, and responses of the *Avena* coleoptile. This year very little was heard of these responses, although they still remain as standard methods of testing chemicals for physiological activity. No one method can be used for all purposes. Had we clung to one method much of what we now know about growth-regulating substances would have been lost.

In the spring of 1935 there were only a few well recognized active substances—indoleacetic, auxins A and B being the most talked of. It is now doubtful if auxins A and B actually exist, but there are literally hundreds of other substances to take their place.

There is still some feeling and controversy over the meaning of terms and definitions of physiologically active substances. Regardless of the original intention for the meaning of the word "auxin," it is now generally considered synonymous with "plant hormones" and "plant growth-regulating substances." The term "growth substance" probably should be reserved for vitamin-like substances essential for growth of lower organisms.

Owing to the varied types of responses induced by plant hormones, the subject drew the attention of botanists, horticulturists, and chemists. Professors at universities found the field a fertile one for graduate students and assigned many projects for theses on this subject. Publications started pouring out and have increased since 1935 to the point where it is difficult to keep up on the subject.

No one person or group of persons could ever have discovered all the facts that are now known about plant growth hormones. Through fear, suspicion, interest, or curiosity one worker picks up where another leaves off and advances our sphere of knowledge. However, no man's word is law. All claims must be tested and proved before they are acceptable in science.

[1] Address of the retiring President of the Torrey Botanical Club presented at the annual meeting on January 7, 1947.

Interest in the subject of plant hormones from the standpoint of fundamental science is still uppermost in the minds of many workers. It is increasingly evident, however, that an attack of practical problems in this field also contributes to fundamental science. It may be said that when practical problems are properly studied, the results of the investigation contribute to both science and practice. In the beginning most of the responses induced by plant hormones were looked upon as laboratory curiosities. It was not long, however, until most of these curiosities led the way to practical applications.

News writers pounced upon curiosities to arouse the interest of the public. They gave much publicity to our so-called upside-down plants, meaning that when tops were removed and plant hormones applied, roots grew on the wrong end of the plant. Leaves, flower petals, peduncles, and petioles all produced roots, making odd-looking plants. Out of these monstrosities, however, came practical methods for propagation of plants. Difficultly propagated species were caused to form roots on cuttings. Easily rooted species were accelerated. Amateurs and practical growers alike now depend upon hormones for propagation of plants.

Ethylene gas induced curvatures on plants and caused leaves to fall. Apples give off ethylene. Therefore, apples placed in storage with rose plants caused the leaves to fall. Ethylene gas and perhaps other chemicals can and will be used by growers to defoliate their plants before they are put into permanent storage. Defoliation is often desirable to prevent loss of moisture and spoilage.

Contrasted to defoliation with ethylene gas is the fact that naphthaleneacetic acid prevents abscission of leaves. This discovery soon led to the practical application, now well known, that naphthaleneacetic acid prevents pre-harvest drop of apples.

The following established practices are now well founded and have resulted from plant hormone research:

Prevention of pre-harvest drop of apples with naphthaleneacetic acid.

Increased fruit set and induced seedless tomatoes with numerous hormone-like substances.

Inhibition of buds to prevent potatoes from sprouting by the use of vapors from esters of naphthaleneacetic acid.

Inhibition of fruit tree buds to prevent loss through late frost, though the method is not yet perfected.

Regulation of flowering of pineapples involving acetylene, naphthaleneacetic acid, naphthoxyacetic acid, and substituted phenoxy compounds. In this way a crop can be staggered to facilitate harvest and canning operations.

Defoliation of plants with ethylene, acetylene, propylene gases, and other chemical means.

Thinning of fruit, especially apple, with hormone sprays, bringing about better quality of fruit and causing biennial-bearing trees to become annual-bearing.

Inhibition and killing of plant tissue, leading to the use of highly active plant hormones as herbicides, for which 2,4-D has been highly publicized.

One of the best illustrations of growth-regulation of plants is the modification of the pattern of new organs growing under the influence of applied hormone-like

chemicals. Substituted phenoxy, benzoic, and naphthoxy acids are particularly effective for this purpose. Mature organs do not change their shape, but all new growth which occurs under the new chemical influence is modified. This leads to the assumption that normal leaf patterns are determined by the natural chemical influences within the plant. Under new and stronger chemical influences the leaves and other organs assume a new pattern. So far no practical application for this odd response had been found. However, we should not be surprised if one crops up, since nearly all facts eventually find some practical use. At least, induced formative effects afford a subject for speculation, to which botanists are so well adapted.

To date no hormone-like chemicals or any one chemical alone has been found to stimulate growth of the entire plant in the same sense as is recognized for complete fertilizers. Some claims for such have been published, but they have not stood the test of time.

Flowers of solanaceous plants last abnormally long after being treated with hormone-like substances which induce parthenocarpic development. This fact is very suggestive and gives immediately the idea that the life of cut flowers can be prolonged. Unfortunately, to date these phenomena seem to apply only to intact plants. No effective chemical means for increasing the life of cut flowers have been discovered.

From our experience with root-inducing substances, modification of leaves, etc., it appears evident that all organs of the plant are under some regulating influences, probably of a chemical nature. It would seem therefore that we should find *flower-inducing substances* and *shoot-inducing substances*. While there have been various claims for shoot-inducing substances, this is not a reality in the same sense that we have root-inducing substances. It is logical, however, to assume that such chemicals do exist in nature and eventually may be found. Once they are located, if they ever should be, progress and spectacular results with such substances should be as outstanding as with well known hormone-like substances.

If we may predict something for the future of plant hormones, we should list some of the following:

Induction of shoots where they do not normally appear, thus facilitating the propagation of plant parts without buds. For example, internodes do not normally produce adventitious buds. A shoot-inducing substance applied to an internode should cause new shoots to arise where desired to make possible propagation of budless parts or to improve the shape and appearance of intact plants.

Flower-forming substances which are thought to exist in nature may be isolated, identified, and used as a common tool. If this becomes a reality it should be possible to force long-day types to flower during the short days or short-day types to flower during long days. In short, it should be possible to induce flowering of plants at will and to force flowers at unusual places. Imagine plants with flowers on internodes, on leaves, and even on roots.

At the present time there appears to be considerable variation in time of ripening of fruit. Under the influence of chemicals, the time of ripening should fit into our needs. Certain varieties of English holly growing on the western coast, though very prolific, fail to ripen berries in time for the Christmas trade. It is conceivable that with the proper treatment this variety can be caused to ripen its fruit so that it will be useful at Christmas time. During the past season it has been shown that apples

treated with certain hormone-like chemicals ripen prematurely. In a lesser degree this has been noted for tomatoes. The tomato flavors are not affected under the influence of the chemical. Apples, however, change flavor and consistency, but the very fact that modifications in time of ripening have been demonstrated, offers encouragement for practical methods applicable to all fruits.

Since it has been demonstrated that fruit buds can be delayed through treatment with growth substances, one is led to the assumption that fruiting of tropical species and flowering of plants in general can be staggered to extend throughout the entire season. Mangoes, for example, flower and ripen fruit at very definite periods of the year. During the rest of the year they are not available as food. Since this is an important tropical food, it would be desirable to extend it throughout the season. This should become a reality by the proper hormone applications to growing buds. The idea is particularly applicable to tropical plants because the temperature and other growing conditions would not limit the time of fruiting. We should, however, be able also to stagger flowering of spring shrubs in the north so that we could enjoy them over longer periods.

From the fundamental research angle many workers are trying to find how hormones work. Much emphasis is being placed on enzymatic activities, precursors, and ultimate active substances. There still remains in the minds of many people the idea that the so-called natural plant hormones are necessary for growth. In contrast to this, however, there are those who believe the so-called hormone-like substances are by-products of metabolism and that they play no important rôle in natural growth. These questions remain to be answered in the future, but they will in all probability be answered. Solutions for problems of this sort will contribute much toward our understanding of botanical sciences.

Proceedings of the Club

Minutes of the Meeting of October 16, 1946. Dr. Zimmerman opened the regular meeting of the Torrey Botanical Club at 3: 30 p.m. at The New York Botanical Garden. Twenty members and friends were present. The minutes of the previous meeting were approved as corrected. Two annual members and 19 associate members were unanimously elected.

It was recommended that the memorial to the late Dr. R. A. Harper be published in Torreya. (See p. 87 of the January issue of the Bulletin.)

There was no further business to transact and the meeting was turned over to Dr. Sophia Satina who spoke on: "Chimeras among Plants and How They Arise."

The meeting adjourned at 4: 45 p.m., and refreshments were served by members of the staff of the Garden.

Respectfully submitted,
Libero Ajello
Recording Secretary

Minutes of the Meeting of November 6, 1946. The regular evening meeting of the Torrey Botanical Club was called to order by Dr. Zimmerman at 8: 15 p.m. at Hunter College. Sixty members and guests were present. The minutes of the previous meeting were approved as read. Four associate members and one annual member were unanimously elected.

Several proposed amendments to the Club's constitution were read and the members voted that the amendments be referred to the Council for further action.

Since there was no further business, the meeting was turned over to Dr. John A.

Small who gave an enlightening lecture on: "The Pine Barrens of New Jersey," illustrated with many fine Kodachromes.

The meeting adjourned at 9: 40 p.m. and was followed by refreshments served by members of the Hunter College Biology Department.

Respectfully submitted,
LIBERO AJELLO
Recording Secretary

Minutes of the Meeting of November 20, 1946. The regular afternoon meeting of the Torrey Botanical Club was opened by Dr. Zimmerman at 3: 30 p.m. in the members' room of The New York Botanical Garden. Thirty members and guests were present. The minutes of the previous meeting were approved as read.

Dr. Zimmerman asked the members to give thought to the proposed compilation and publication of a cumulative index to the first 75 volumes of the BULLETIN of the Torrey Botanical Club and to present any suggestions that they may have on the subject.

Dr. Simpson brought to the attention of the members an error in the opening time of the December 18th meeting as listed in the *Bulletin* of the New York Academy of Sciences. The correct time for the meeting is Wednesday afternoon, December 18th, at 3: 30 p.m. at The New York Botanical Garden.

No further business was transacted and the meeting was turned over to Dr. W. C. Price, who spoke on "The Isolation, Identification and Characterization of Southern Bean Mosaic Virus."

The meeting was adjourned at 4: 50 p.m. and was followed by refreshments served by members of the Staff of The New York Botanical Garden.

Respectfully submitted,
LIBERO AJELLO,
Recording Secretary

Minutes of the Meeting of December 3, 1946. The regular evening meeting of the Torrey Botanical Club was opened by Dr. Zimmerman at 8: 10 p.m. at Columbia University. Twenty members and guests were present. The minutes of the previous meeting were approved as read. The names of two prospective annual members were presented to the Club and both were unanimously elected to membership.

No further business was transacted and the meeting was turned over to Dr. M. F. Buell, who spoke on "The Ecology of the Carolina Bays." The speaker's abstract follows:

> There are four principal hypotheses concerning the origin of the Carolina Bays:—the meteorite hypothesis of Melton and Schriever, the hypothesis of complex origin by Douglas Johnson, the lagoon hypothesis of C. W. Cooke, and the biological hypothesis of Chapman Grant. The plant ecologist, particularly through paleoecological studies, can contribute knowledge of the bays that may have considerable value in deciding the validity of these various hypotheses. Reconstruction of vegetation recorded by pollen grains preserved in the bottom sediments, in other words the vegetation existing during the early development of the lakes which occupied the depressions, is particularly important. This includes both bog vegetation and the vegetation of the surrounding upland. The bottom sediments of one bog have been studied. They contain pollen representing boreal species with a corresponding absence of southern species. This suggests a colder climate than that which now prevails in the region of the bays. In fact, it suggests that this particular bay may have been formed in late Pleistocene time. Further studies on the bays should reveal whether or not they were all formed at about the same time.

The meeting was adjourned at 9: 35 p.m. and was followed by refreshments served by members of the Columbia University Botany Department.

Respectfully submitted,
LIBERO AJELLO,
Recording Secretary

Minutes of the Meeting of December 18, 1946. The regular afternoon meeting of the Torrey Botanical Club was opened by Dr. Zimmerman at 3: 40 p.m. at The New York Botanical Garden. Twenty members and guests were present. The minutes of the previous meeting were approved as read.

Dr. Seaver moved that the Club publish a cumulative index to the first 75 volumes of the BULLETIN of the Torrey Botanical Club, as a memorial to Dr. and Mrs. Britton. The motion was seconded and carried unanimously by the members.

No further business was transacted and the meeting was turned over to Dr. Ray Dawson, who spoke on "Corn and Pellagra—A Botanical Approach to a Problem in Human Nutrition."

The meeting was adjourned at 4: 25 p.m. and was followed by refreshments served by members of the staff of The New York Botanical Garden.

Respectfully submitted,
LIBERO AJELLO,
Recording Secretary

Minutes of the Annual Meeting, January 7, 1947. The annual dinner meeting of the Torrey Botanical Club was held on the evening of January 7th at the Men's Faculty Club of Columbia University. There were 80 members and friends present. Following the dinner, the business meeting was called to order by Dr. Zimmerman at 7: 30 p.m. The minutes of the previous meeting were read and approved. Sixteen annual members and five associate members were elected to membership in the Club.

The following officers and chairmen of standing committees made reports which are attached to the minutes:

Dr. J. A. Small, *Chairman of the Field Committee*
Dr. H. W. Rickett, *Editor*
Dr. A. M. Hanson, *Business Manager*
Dr. J. L. S. Simpson, *Corresponding Secretary*
Dr. E. H. Fulling, *Treasurer*
Dr. M. Levine, *Chairman of the Membership Committee*
Dr. A. H. Graves, *Chairman of the Special Committee on Fungi*
Mr. L. Ajello, *Recording Secretary*

Dr. P. W. Zimmerman, as retiring President, gave a stimulating address on "Plant Hormones," which is printed elsewhere in this issue of the BULLETIN.

After this talk, Dr. E. B. Matzke announced the results of the mail ballot for officers for 1947 as follows:

President—Dr. George H. Shull
1st Vice-President—Mr. Rutherford Platt
2nd Vice-President—Dr. Norma E. Pfeiffer
Corresponding Secretary—Dr. Jennie L. S. Simpson
Recording Secretary—Mr. Libero Ajello
Treasurer—Dr. E. H. Fulling
Editor—Dr. Harold W. Rickett
Bibliographer—Mrs. Lazella Schwarten
Business Manager—Dr. Harold H. Clum
Members of the Council—Dr. W. H. Camp, Miss Hester M. Rusk, Dr. Michael Levine, Dr. John S. Karling
Delegate to the Council of the N. Y. Acad. of Sciences—Dr. Edwin B. Matzke
Representatives on the Council of the A. A. A. S.—Dr. Michael Levine, Dr. George S. Avery
Representative on the Board of Managers of The New York Botanical Garden—Dr. Fred J. Seaver

Dr. Karling moved that the officers elected by ballot be approved. The motion was seconded and carried unanimously.

The meeting was then turned over to Dr. George H. Shull who spoke a few words of greeting to the Club.

The meeting was adjourned at 9: 00 p.m.

Respectfully submitted,
LIBERO AJELLO,
Recording Secretary

FIELD TRIP REPORTS

AUGUST 4. SINGAC, N. J. Undaunted by an overcast sky, which later cleared, ten intrepid Torreites and guests embarked in canoes on the Passaic River. At Two Bridges the left fork of the river was chosen for exploration. This branch meanders tortuously for many miles. There was time, however, to reach only a distance of 5 or 6 miles as the crow flies, for our botanical explorers made frequent stops and side trips into coves which penetrated the low meadows.

From the botanical viewpoint the trip was moderately interesting. The banks of the Passaic were fringed with common deciduous trees: several species of *Quercus, Betula nigra* plentifully, more *Acer saccharinum* (Silver Maple) than *A. rubrum*, occasionally *Fraxinus pensylvanica, Tilia americana, Salix nigra, Ulmus americana, Liquidambar, Platanus, Fagus, Carpinus*, and other genera. The shrubs, *Cornus amomum, C. racemosa, Cephalanthus*, and *Leucothoë racemosa* were also noted. Naturally, there were abundant festoons of Poison Ivy. The shores of the Passaic were rich with the Tall Indian Rice, *Zizania aquatica*, which was common throughout and sometimes invaded quite far into the river. At the time of this visit it littered the waters with the fallen staminate flowers. Other shore species noted growing on the mud near the water line were *Pontederia cordata, Nymphaea advena, Sagittaria latifolia, Alisma subcordatum, Saururus cernus, Sium suave, Gratiola neglecta*, and *Lindernia dubia* var. *inundata*.

Lindernia (*Ilysanthes*) and *Gratiola* have a superficial similarity, but can be told apart easily with some casual examination. *Lindernia* is glabrous, whereas *Gratiola neglecta* is glandular puberulent above; the calyx in *Lindernia* is distinctly 5-parted, whereas that of *Gratiola* seems to have 7 unequal parts because of the two bractlets which subtend the calyx-lobes. *Rumex mexicana* was quite abundant throughout the entire stretch of the trip. *Lysimachia* (*Steironema*) *hybrida* was seen several times. For the nomenclature of this species see Fernald, "The identity of *Lysimachia lanceolata*" (Rhodora 39: 438–442. 1937). Fernald here claims that Handel-Mazzetti shows that the characters relied upon to keep American *Steironema* apart break down in some Chinese species of *Lysimachia*, and that *Steironema* cannot be treated as a different genus. Fernald also points out that *L. lanceolata* is a southern plant, whereas the northern species is *L. hybrida*.

Polygonum robustius was not yet in flower, while *P. punctatum* was fully so, its slender racemes erect. These two species, in their different periods of flowering, as well as in other respects, appear as distinct entities, notwithstanding their synonymous disposition in Gray's Manual, 7th ed. *P. hydropiper* var. *projectum*, in its nodding racemes, larger red stem and broader leaves, was seen to differ from *P. punctatum* even at a distance. One of the most showy flowers was *P. pensylvanicum* (the common form with leaves glabrous beneath, named var. *laevigatum* by Fernald). Their tall bright rosy-red racemes often made a splendid back-drop for the bank's margin. Occasionally *P. lapathifolium* was noticed nearby. It was the form with nodose joints and pale, more slender, drooping racemes, and it looked like an unfortunate relative of the former species. Adding color to the floral display, usually in the more open places, were *Asclepias incarnata, Spirea latifolia, S. tomentosa, Stachys hispida*, and *Vernonia*. In a meadow, where the group stopped to explore on foot, were noted *Iris prismatica, Pycnanthemum muticum, Scutellaria integrifolia, Polygala sanguinea, Oenothera tetragona*, and *Galium tinctorium*. Concerning the last plant mentioned, Hiroshi Hara (Rhodora 41: 388. 1939) claims that *G. tinctorium* is part of a circumpolar species differentiated into 3 geographical varieties or subspecies and names ours *G. trifidum* subsp. *tinctorium*.

The aquatic flora was also generally the common type. Several species of *Potamogeton*, tons of *Zosterella* (*Heteranthera*) *dubia* and *Vallisneria americana*, frequent ex-

amples of *Ceratophyllum*, and occasional *Castalia odorata* were seen. Of particular interest was the Thong-leaved Sagittaria, with its long slender phyllodia up to 1 meter long and 10 mm. wide and small floating flowers. This plant is named *S. lorata* in the "Illustrated Flora" and *S. subulata* var. *gracillima* in Gray's "New Manual of Botany," Fassett's "A Manual of Aquatic Plants" and Muenscher's "Aquatic Plants of the United States." It is well illustrated in both Britton & Brown's "Illustrated Flora" and Fassett's "Manual." As observed on the Passaic, the plant has all the appearances of a distinct species.

Homeward bound, on the way to Little Falls, the comparison of *Centaurea nigra* and *C. jacea* arrested the group's attention somewhat. It was noted that while *C. nigra* was already past blooming, *C. jacea* was at its flowering peak. These species belong to a section of *Centaurea* which is badly understood. Our observation indicated that these two, at least, behave like distinct species.

Two suggestions are made for botany students concerning the plants seen on this trip: that a critical field study be undertaken of the local *Centaureas*, particularly of the forms or varieties of *C. nigra*, *C. jacea*, and *C. vochinensis*, and that a detailed investigation be conducted on the identity of the Thong-leaved Sagittaria. A repetition of the trip by the Torrey Botanical Club is recommended for the future.—JOSEPH MONACHINO, Leader.

AUGUST 31–SEPTEMBER 2. BOTANICAL SURVEY and check of guidebook material between Culvers Gap and Harding Lake, N. J. A list of species was prepared for the record. Attendance 6. Leader, L. E. Hand.

SEPTEMBER 7–8. MT. EVERETT, MASS. The striking summit, locally known as "The Dome," with its scrub vegetation and rock plants was studied. A pond and a woodland with their contrasting flora were likewise examined. A small group made a flying trip to Bartholomew's Cobble, an area much desired for permanent preservation by the Trustees of Public Reservations. No list was kept but the Gray Herbarium has been instrumental in listing plants of the Cobble, of which we have copy. It is hoped that someone will offer a trip primarily to the Cobble soon. Attendance 21. Leaders, Rutherford Platt and Harold N. Moldenke.

SEPTEMBER 8. INWOOD PARK, N. Y. "The various species of trees and shrubs were seen and listed and a striking specimen of *Triosteum aurantiacum*, the Horse Gentian, with clusters of orange fruit, was seen; the small species of Wild Geranium was common." Attendance 18. Leader, Arthur H. Graves.

SEPTEMBER 14–15. FORKED RIVER, N. J. Five different walks probed the interesting countryside, and bayside. As usual here, additions were sought to the present list of recorded plants. These lists from 1944 and 1945 are now available in mimeographed form upon request to the field chairman. Most of the famous pine barrens novelties were shown to those making the visit for the first time. A good opportunity to learn distinguishing characteristics of asters, goldenrods, and Eupatoriums was afforded. Attendance 33. Leaders, Hollis Koster and L. E. Hand.

SEPTEMBER 15. MAPLE GRANGE VICINITY, SUSSEX CO., N. J. This was another Apppalachian Trail survey trip and added many new names to the list since it was the first visit to limestone country and also extended into non-calcareous areas. The list is available from the files of the field chairman but it has not been mimeographed. Attendance 5. Leader, G. G. Nearing.

SEPTEMBER 22. MILL NECK, L. I. The group enjoyed an interesting walk through forests, fields, salt and fresh water habitats. One individual specialized in a search for rusts while others paid more attention to the higher plants and passing birds. Attendance 16. Leader, Farida A. Wiley.

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COMPILED BY
LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITOR OF THE TAXONOMIC INDEX

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